SYSTEMATIC ANATOMY OF THE DICOTYLEDONS

A HANDBOOK FOR LABORATORIES OF PURE AND APPLIED BOTANY

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TO

PROF. DR. L. RADLKOFER

SEINEM HOCHVEREHRTEN LEHRER UND VORSTANDE

THIS BOOK IS DEDICATED

BY THE AUTHOR

EDITORIAL PREFACE

Professor Solereder's prefaces, to the original German edition and to the present English translation, explain so clearly the object and scope of his book that it is unnecessary to enter on any further detailed exposition of its purpose.

The work is universally recognized among Botanists as the standard authority on the subject of the anatomy of plants as applied to systematic purposes; though limited to the Dicotyledons, Professor Solereder's book must serve as the type of all treatises dealing with the structure of other classes from a similar point of view. Covering, as it does, with marvellous completeness and exactitude, the most extensive and important division of the Vegetable Kingdom, the 'Systematic Anatomy' forms an indispensable work of reference to all engaged in systematic studies, and serves at the same time as by far the best source from which students may gain an idea of the objects and methods of this young and vigorous branch of Botany.

Until recently, the study of anatomical structure in relation to taxonomy has been but little pursued in this country, though a beginning was made, many years ago, by some of our greatest systematists. The present translation will, it is hoped, much facilitate the introduction of modern anatomical methods into the daily work of the Herbarium and the Economic Museum. One of the advantages of the study of systematic anatomy is that it brings together the work of the laboratory botanist and the taxonomist, each of whom has hitherto often remained too much isolated in his own department.

The case for the anatomical method is put by the author with singular judgement and moderation, as will be seen from the Introduction and the Concluding Remarks. The latter form a very full and valuable summary of the various anatomical characters and their value in classification; they may be read with interest and advantage by all students of botany, whether their bent be systematic or otherwise.

It may be pointed out that the English edition has been brought thoroughly up to date, both the Addenda and the Concluding Remarks having received from the author's hand all the emendations which will be embodied in the new German edition.

The work of translating so extensive a treatise, embracing such a vast amount of minute and accurate detail, has naturally been extremely arduous; and the translators, Mr. Boodle and Dr. Fritsch, are to be congratulated on the successful completion of their labours. The translation, first begun by Mr. Boodle, was carried out jointly by him and his colleague up to the end of the Natural Orders; the work of translating the Addenda and Concluding Remarks fell to Dr. Fritsch alone.

My own part has consisted in the revision of the proofs throughout, and in the necessary consultations with the translators on all questions that arose in the course of their work. I have aimed at securing a sufficient uniformity of style throughout the book, and have satisfied myself that the translation faithfully conveys the author's meaning. The rendering of technical terms has in some cases presented a certain amount of difficulty; it is proposed to add a glossary of the less familiar terms, with their German originals, at the end of the second volume.

Some additional references to the literature, which came in too late to be appended to the lists under each Natural Order in the Addenda, will be found collected at the end of the book.

D. H. SCOTT.

March 31, 1908.

PREFACE BY THE AUTHOR TO THE ENGLISH EDITION

The present English edition of the 'Systematische Anatomie der Dicotyledonen,' originally published in the year 1899 by F. Enke in Stuttgart, contains the translation of the Introduction and of the Anatomical Characters of the Dicotyledonous Orders (pp. 1–903 of the German edition). This, the principal part of the book, is followed by an appendix, compiled at the request of my English colleagues, which summarizes, under the respective Orders, the results of recent researches. The book terminates with the 'Concluding Remarks,' which give a survey of the anatomical characters of the vegetative organs and of the distribution of these characters among the Dicotyledons, and constitute a revised treatment of the 'Schlussbemerkungen' of the original German edition (pp. 904–79).

As regards the arrangement of the subject-matter and the terminology of the species, exactly the same plan has been followed in the Addenda as in the principal part of the book (see the preface to the German edition). The Orders are dealt with in the sequence of Bentham and Hooker's system. In the descriptions of the individual Orders supplementary details to the 'review of the anatomical features,' the 'structure of the leaf,' the 'structure of the axis' and in some cases also the 'structure of the root' succeed one another. In the sections devoted to the structure of the leaf and the structure of the axis the anatomical characters are discussed in the same serial order as in the principal part of the book. A considerable amount of trouble has been taken in completing the references to literature; papers, of which I was acquainted with the title only or of which only abstracts were available, are again placed in square brackets. Readers who are conversant with the subject will also find new observations, which have not yet been published elsewhere, introduced from time to time.

In concluding, I should like above all to express the pleasure which the translation of my book has afforded me, for it carries with it the hope that the anatomical method will find new adherents, who are so necessary for its further elaboration and obligatory introduction into all systematic researches (monographs, questions of affinity, establishment of new genera and species). At the same time I wish to tender my heartiest thanks to the translators for the great labour expended on the preparation of this work, as well as to the Delegates of the Clarendon Press for their invariable readiness to meet my wishes, and,—last not least,—to all the colleagues who have assisted me in my work by the forwarding of separate copies or of material for investigation.

H. SOLEREDER.

ERLANGEN,
October, 1907.

PREFACE

TO THE GERMAN EDITION

'THE next hundred years will be devoted to the anatomical method;' these significant words of an illustrious Botanist[1] are directly responsible for the production of this book. Repeated earlier attempts had been made to employ the characters afforded by the anatomy of the vegetative and reproductive organs, in conjunction with external features, for systematic purposes, and for a long time such characters had been of service to those engaged in applied science as a means of determining vegetable products. Both De Candolle and Endlicher had found anatomical characters useful in the division of the Phanerogams into the two great groups, the Monocotyledons and Dicotyledons. It is only in recent times, however, that certain well-known investigators, and foremost among them Radlkofer, have succeeded in demonstrating in a convincing manner the scientific value of anatomical characters for systematic purposes, and in founding an anatomical method. With the help of this they have been able to solve systematic problems which otherwise could scarcely have been elucidated, and to throw an essentially new light on scientific questions relating to the delimitation of species, genera and Orders, as well as to natural affinities. Considering these brilliant results it is not surprising that small success attended the opposition of systematists of the old school, who were averse to the unaccustomed use of the microscope in this department of Botany, and feared lest they should have to resign their favourite science to their younger, initiated colleagues; and it is not to be wondered at that the new method gained a sound footing. On the other hand, it is not unnatural that a number of Botanists of the new school expected too much from the anatomical method, and not only looked for a revival of systematic Botany on a surer foundation, but also for an entirely new Natural System.

Now that nearly a decade and a half have elapsed since Radlkofer's memorable speech was delivered, and hundreds of papers have been published affording numerous data on the value of anatomical characters considered generally or within the limits of certain Orders, the time appears to have come for summarizing the results attained, and, with the aid of the data which have been established, for forming a decision as to how far our expectations of the anatomical method have been justified.

Having been trained in Radlkofer's school of Botany, my own scientific researches, as well as a study of the literature of the subject and the share in the direction of Radlkofer's laboratory entrusted to me, imbued me with a keen interest in the development of the new line of systematic anatomical investigation—first elevated by Radlkofer to the rank of a scientific method. As a consequence I have for many years realized the need for a summary of

[1] Radlkofer, Ueber die Meth. in d. bot. Syst. insbes., d. anat. Methode. Festrede, Munich, 1883.

the results acquired, and have desired to undertake the work. I therefore gladly accepted the publisher's invitation to write a book on this subject. It cannot be expected that the value of this work will rise to the level of the high aims of the anatomical method, notwithstanding the great amount of labour expended by me on the study of the various treatises (which sprang up like mushrooms!), on the re-investigation of doubtful statements, and on numerous supplementary investigations of my own, which a reader conversant with the subject will find scattered here and there. It was not possible to give the different Orders a completely uniform treatment, since the investigations were not always equally thorough; in those cases in which only preliminary statements were available, it was necessary to quote them in some detail, in order to avoid generalizations, and to enable the reader to appreciate the gaps in our present knowledge. The prolonged period during which this work has been in course of preparation may also form an excuse for such inequalities of treatment as have been retained. As a result of my honest endeavours, however, I think I may say that this book gives a review of the results hitherto obtained, and will thus form a basis for future supplementary investigations, and a useful handbook for those concerned with systematic problems. It will also be of value in applied Botany, inasmuch as the economic Botanist had hitherto no handbook for the determination of raw vegetable products of unknown origin, and also to the physiologist who wishes to obtain information on the anatomy of the plants used in his experiments, and on the distribution of certain anatomical features which are connected with special functions.

As regards the general plan of the book and the arrangement of the subject-matter in the description of the individual Orders, the following points may be mentioned. The Introduction deals chiefly with the value of the anatomical method and of anatomical characters, and touches on the problems connected with this subject. The Introduction is followed by a description of the anatomical features in the individual Dicotyledonous Orders, the serial arrangement of the latter being the same as in Bentham and Hooker's Genera Plantarum. The description of each Order begins with a short review of the anatomical characters, with the help of which it is possible to determine whether a given plant may be regarded as a member of that Order or not. More detailed statements, forming an amplification of this review, are given in the succeeding sections, which are, as a rule (in the larger Natural Orders), arranged under the headings—'Structure of the Leaf,' and 'Structure of the Axis.' In order to avoid confusion, the different species cited in connexion with the various anatomical features are enumerated, without regard to synonymy, under the names assigned to them by the authors who demonstrated these anatomical characters in the species in question; in those cases in which the specific name is placed between inverted commas, this is done to indicate that I was unacquainted with the name. In the sections on the structure of the leaf and axis the individual anatomical features are taken serially, and certain of them are made prominent by the use of Clarendon type. In this connexion it is only necessary to point out that characters which are common

to the leaf and axis (such as the hairy covering, oxalate of lime and other contents, internal secretory organs, &c.) are in most cases described jointly for both these organs; these features are generally dealt with under the structure of the leaf, since they are more readily observed in the leaf, and have consequently been examined for the most part with special reference to that organ. Statements on the structure of the root are occasionally appended to the section on the structure of the axis. In general, however, the root is not dealt with in detail, because the existing researches on this subject are not sufficiently comprehensive, owing to the difficulty in procuring material, while the results obtained are not of any special consequence in the diagnosis of an Order. At the end of the description of each Order there will be found a list of the papers published up to 1898; these form the basis of the statements included under the Order, and from them the reader may obtain further information. The arrangement of the references in these lists of literature is chronological; as a rule the titles of the papers are quoted in an abbreviated form, and only such as contain no more than a few isolated data are omitted; papers, of which I was acquainted with the title only, are placed in square brackets. The principal part of the book is followed by the 'Concluding Remarks'; these constitute a summary of the existing data in the form of an enumeration of the anatomical characters, which are considered in relation to their systematic value: the Concluding Remarks together with the Introduction may also serve as a guide to the anatomical method.

In the use of this book a knowledge of plant-anatomy is taken for granted. Readers requiring information on this subject may, besides using the ordinary botanical textbooks, consult such works as De Bary's Vergleichende Anatomie der Vegetationsorgane, translated in this series, Haberlandt's Physiologische Pflanzenanatomie, Tschirch's Angewandte Pflanzenanatomie, or Van Tieghem's Traité de Botanique, vol. i.

In concluding this preface I wish to express my warmest thanks to all those who have assisted me in the publication of this book. Above all I am indebted to Professor L. Radlkofer, to whom I dedicate this book with grateful veneration. I am also deeply indebted to the Königlich Bayerische Akademie der Wissenschaften, who favoured my work with material assistance, and to the Directors of the Königliche Hof- und Staatsbibliothek in Munich, whose generosity enabled me to make ample use of the valuable books contained in the library; I also wish to express my thanks to Professors Goebel, Urban, Schenck and Volkens, and to other colleagues, who assisted me either in obtaining literature or by granting permission to make use of a large number of illustrations in their published works, and to Herr Dunzinger, who drew a number of the original figures from my preparations. Lastly, I wish to thank the publisher for the care he has bestowed on the production of this book. I trust that it may prove worthy of the valuable assistance which I have received.

THE AUTHOR.

MUNICH.

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INTRODUCTION

THE anatomical method[1] consists in the methodical employment of the micro-anatomical and micro-chemical characters of the vegetative and reproductive organs in systematic researches.

For a long time anatomical characters have been made use of in the determination of plants. Apart from the fact that those concerned with pharmacology, palaeophytology, forestry, and more especially cryptogamy, have employed them in the identification of their material, systematists, dealing with the higher plants, have from early times made use of such characters—almost unawares—in conjunction with external features. The phrases 'folia pellucide punctata,' 'folia subtus opaca,' 'nervi immersi vel elevati,' and others like them, occurring in their descriptions, are merely the expression of definite anatomical features, although lacking that sharp precision which can only be attained by the use of the microscope. The innovation, due to the anatomical method, however, lies in the use of the microscope—formerly the instrument of the physiological botanist only—in systematic researches, and further consists in the methodical anatomical investigation of one species after another.

The actual idea of employing the internal structure for systematic purposes originated in very early times and has repeatedly been put forward. To quote an early example: Linnaeus, in the 'Genera Plantarum' (Ratio operis, under 5), hints at its employment for specific diagnosis in the words 'Ergo species tot sunt, quot diversae formae *seu structurae* plantarum . . . hodiernum recurrunt.' Again, in De Candolle's and Endlicher's systems we find anatomical features of the stem employed for the distinction of the groups of plants now termed Monocotyledons and Dicotyledons, and in Martius's description of the Coniferae the nature of the wood is included in the diagnosis. Since the time of the two Jussieus, stress has been laid not only on the occurrence of endosperm in the seed, but also on its nature with reference to starchy or oily contents; that is to say, the systematic significance of micro-chemical characters had already been recognized. Mirbel and Chatin went much further. The first of these authors, in the Ann. du Mus., t. xv, 1810, distinctly expresses the opinion that comparative anatomy will play an important part in perfecting the Natural System of plants.

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[1] Literature: Radlkofer, Ueber d. Methoden in d. bot. Syst., insbes. d. anat. Methode, Festrede, München, 1883.—De Bary, Vergl. Anat., 1877, p. 26.—Vesque, in Nouv. Arch. Mus. d'hist. nat., t. iv, 1881, p. 1, Ann. sc. nat., sér. 6, t. xiii, 1882, p. 1 and t. xv, 1883, p. 105, Compt. rend. 1883, p. 1866, Ann. agron., t. x, 1884, p. 14, Bull. Soc. bot. de France 1889, p. xli, and Bot. Centralbl. 1890, i, p. 344, Feuilles des jeunes natural., 1889–90, n. 229–38, Suites au Prodr., vol. viii, 1893, p. 6.—*Engler, in Bot. Jahrb., Bd. v, 1884, p. 142, and in Syllabus, 1892, p. ix.*—Gérard, Anat. comp. végét. appl. à la classificat., Thèse, Paris, 1884.—K. Richter, Bot. Systematik, 1885, especially p. 165.—Schwendener, Richt. u. Ziele d. mikrosk. bot. Forsch., Rekt.-Rede, Berlin, 1887, p. 9, and in Sitz.-Ber. Berl. Akad. 1889–90.—Valeton, De anatomische Methode etc., in Progr. Gymnas. te Groningen 1888.—Westermaier, Wiss. Arb. d. bot. Inst. d. Univ. Berlin 1888, and in Monatsber. Berlin. Akad. 1881, p. 1051.—Vuillemin, in Bull. Soc. bot. de France 1889, p. xc.—Scott, 'On some progress in our knowledge of the anatomy,' etc., Ann. of Bot., vol. iv, 1889, p. 147.—Bertrand, Des caractères que l'anat. peut fournir à la classificat., etc., Autun, 1891.—P. Schumann, Grenz. d. Variation, etc., Bot. Centralbl. 1891, i, p. 357, and ii, p. 1.—Gilg, in Engler, Bot. Jahrb., Bd. xviii, 1894, p. 554.—Parmentier, Ann. sc. nat., sér. 8, t. ii, 1896.

His attempts were not very encouraging, as they were chiefly concerned with certain anatomical features of the stem, which are of little value for systematic purposes. Chatin ('Anat. comp. végét. appl. à la classificat.,' Thèse, Paris, 1840) repeatedly put forward views similar to those of Mirbel, and his 'Anatomie comparée des végétaux' (1856–1870), which remained uncompleted, is the result of his endeavours. In the other anatomical works, which appeared in large numbers during this period, no account was taken of taxonomy, except in Régnault's treatise on the Cyclospermae (Ann. sci. nat., sér. 4, t. xiv, 1860) and in some few others,—whilst scarcely any systematist made use of anatomical characters, or, if employed, they were always such as are easily determined with the help of a lens, e.g. cystoliths, which Wedell took into consideration in his monograph of the Urticaceae, published in 1856 (Arch. du Mus., t. ix). The following works essentially paved the way for the development of the anatomical method: that of Duval-Jouve on the French species of *Equisetum* (Paris, 1863), in which anatomical characters are made use of in distinguishing the species, and which led to other works by the same author[1], undertaken on the same lines, and to Bertrand's treatise on the anatomy of the branches and leaves of the Gnetaceae and Coniferae (Ann. sci. nat., sér. 5, t. xx, 1874); Bureau's notable treatise (Bull. Soc. bot. de France, 1872), in which the anomalous structural features and other anatomical characteristics of the axis of the Bignoniaceae were utilized in the diagnoses of the genera; Engler's studies on the affinities of the Rutaceae, Simarubaceae and Burseraceae (Halle on the Saale, 1874), in which a natural delimitation of these orders was initiated with the aid of the internal secretory organs; and above all, Radlkofer's monograph of the Sapindaceous genus *Serjania*, which after long preparatory work (see Report of the British Association for the advancement of Science, Norwich, 1868, &c.) appeared in the year 1875. Radlkofer undertook the investigation of the stem and of certain anatomical features in the leaf in species after species and showed in a convincing manner that the adoption of anatomical characters in classification was not merely a possibility but a necessity; owing to his systematic and unprejudiced mode of procedure he is to be regarded as the actual founder of the anatomical method. Not long afterwards the various works of Vesque appeared, and the development of the anatomical method owes much to this investigator, who especially favoured the employment of the leaf-structure for systematic purposes. The works of Radlkofer and Vesque were succeeded by innumerable researches, since the new field of work offered abundant material for investigation and gave gratifying results. In one case an anatomical character was traced through a series of orders, in another a certain group of affinity was accurately examined in all anatomical respects. And now systematists could no longer ignore the new method. At the botanical congress, held in Paris in 1889, the anatomical method was submitted to discussion and Vesque proved to be equally skilled and eloquent in its support. In correspondence with the importance of this method we find anatomical characters taken into consideration in a prominent manner in certain parts of the recent splendid work of Engler and Prantl, 'Die natürlichen Pflanzenfamilien,' which summarizes the advances in systematic botany. In recent systematic treatises published by various authors and dealing with the affinity between different Natural Orders and between different genera, we find anatomical characters placed side by side with the external features. If anatomical characters are not employed at all, or inadequately, or if they are not used in a

[1] See also by the same author, Comp. histotax. et leur import. dans l'ét. crit. des espèces végét., in Mém. de Montpellier, sect. des sc., 1871, and Histotaxie des feuilles des Graminées, in Ann. sc. nat., sér. 6, t. i, 1875.

sufficiently methodical manner (i.e. not in the same way as the external features) by the majority of systematists, this is not due to an underrating of anatomical characters and is only to some extent the result of the preliminary training of the systematic school—for the younger systematists are trained in the new line of research. It is solely a consequence of the method of investigation, which, although far surer, is more laborious and involves a considerable expenditure of time and which systematists cannot, or, one should rather say, are not willing to undertake owing to the large amount of material which is continually submitted to them from all sides. The quantity of work produced must naturally be sacrificed to its better quality, and vice versa. I may take this opportunity of making an urgent appeal to all systematists to take anatomical features into consideration as far as possible, when publishing new genera and species [1]. If this were done the anatomical method might in time acquire a classical basis, from which conclusions could be drawn with more safety than has hitherto been possible.

The work required by the anatomical method is quite enormous. It must, as is expressed in the definition of the term, extend to all organs, both reproductive and vegetative. It is clear that this cannot all be carried out at once. In the first place, therefore, those organs had to be taken into consideration which are most readily obtainable for the practical purposes of systematic botany, viz. for the determination of a given plant. These are the vegetative organs, i.e. leaf and stem. Their investigation in some cases even makes it possible to determine a plant in the sterile condition. Of the two organs, leaf and stem, the leaf has proved to be especially valuable. In the leaf, those anatomical characters which are most essential, such as stomata, hairy covering, internal secretory organs and so on, are most typically developed, and in this part of the plant the most manifold structural variations are to be found, since it has been shown that of all organs this is most subject to adaptations. The search for anatomical characters, which are often concealed or only of isolated occurrence, is most readily undertaken in the leaf, owing to the superficial extension of this organ. If the vegetative organs do not suffice for the solution of systematic problems, the anatomy of the reproductive organs must naturally be taken into account. Since this book is confined to the exposition of the anatomical characters in the vegetative organs, it may be briefly pointed out how useful such features as the structure of the pollen (e.g. in the Acanthaceae and Convolvulaceae [2]), the structure of the pericarp and testa [3], and especially the structure of the endosperm have already proved to be. These, however, are for the most part only casual observations: a methodical investigation of the reproductive organs has not yet been carried out.

According to the above definition, micro-chemical as well as micro-anatomical features must be employed for systematic purposes. The investigations hitherto published are almost confined to the latter. Micro-chemical features have hitherto only been taken into consideration to a small extent, and this is due to the difficulties involved in their determination. At the present time the means afforded by Chemistry are still insufficient to enable us to perform unimpeachable chemical reactions, and the latter are often unsuccessful, because the presence of other substances interferes with or prevents the

[1] An introduction to the use of Latin expressions for anatomical features is found in Vesque, in Suites au Prodr., t. viii, 1893, pp. 15, 16.

[2] See Radlkofer in Sitz.-Ber. Münch. Akad. 1883, p. 256; Lindau in Engler, Bot. Jahrb., Bd. xviii, 1893, p. 36; and Hallier, loc. cit., Bd. xvi, 1893, p. 517. Regarding structure of the pollen of Phanerogams, see Mohl, *Ueber den Bau und die Formen der* Pollenk., Bern, 1834; Fritzsche, Ueber d. Pollen, Mém. Acad. imp. de St-Pétersbourg, 1837; H. Fischer, Beitr. z. vergl. Anat. d. Pollenk., Breslau, 1890.

[3] Amongst others see Harz, Landwirtschaftl. Samenkunde, Berl., 1885, 2 vols.

reaction. Are we not often unable even to demonstrate proteid with certainty by micro-chemical means with the help of any of the numerous reactions for proteid which exist? In addition to this, a further difficulty lies in the fact that the characteristic substances are not always found in all organs of the plant, but are confined to one or other of them and commonly only occur in small quantities. The true value of this section of the anatomical method remains to be determined in the future. For this reason, however, it is well to note the most important facts regarding the present status of this line of research.

The consideration of the chemical substances in the plant for systematic purposes commenced at an early period, and dates back as far as the times of the doctrine of signatures. It was perhaps the only valuable feature in this doctrine, since it sought to characterize a plant by its action on man and by its properties and juices. Linnaeus also had a high opinion of the value of Chemistry, for, in his 'Philosophia botanica' (xii. 337), he says, 'Plantae, quae genere conveniunt, etiam virtute conveniunt, &c.,' and enumerates Genera, Ordines, and Classes, in which the same Vires occur. Finally, a classification of the vegetable substances hitherto found in or excreted from plants [1] affords ample justification for the chemical method. Mucilage, for instance, will be found to be characteristic of the Malvaceae and allied orders; Inulin of the Compositae, Campanulaceae, and other closely related orders, whilst Saponin occurs in the Caryophyllaceae and Sapindaceae; and apart from these cases, the presence of starch or of fatty oil in the seed was recognized as a useful diagnostic character at an early date (see above). Equal importance must be attached to the bitter principles occurring in the Simarubaceae and Gentianeae, the resins found in the Coniferae, the aromatic substances of the Rutaceae and Labiatae, and the occurrence of hydrocyanic acid in the Pangieae. Again, certain alkaloids are especially important and in some cases characteristic of Orders (Papaveraceae, Fumariaceae, Solanaceae), tribes (Amygdaleae, Genisteae), genera (*Cinchona* and *Remijia*, *Delphinium* and *Aconitum*), or a certain group of species (Strychnine in some species of *Strychnos*), whilst in some few cases they occur only in a single species, Santonin being distinctive of the plant from which Flores Cinae is obtained. The examples quoted sufficiently illustrate the fact that the systematic value of the chemical substances varies in the same manner as that of the external organs. The features presented by the latter may be constant for the members of a larger or smaller group of affinity (even as restricted as the species), and the same applies to the chemical substances, present in plants. Moreover, as with external characters, one and the same substance may be found in isolated members of Orders which are widely separated systematically (e.g. allyl sulphide in *Petiveria* (Phytolaccaceae) and in *Sisymbrium*, acid oxalate of potash in *Oxalis* and in *Rumex*), or, on the other hand, in Orders which are closely related, thus constituting additional evidence of affinity (e.g. the occurrence of Amygdalin in the Amygdaleae and in some Leguminosae, or of the narcotic alkaloids, which are found not only in the Solanaceae but also in certain Boragineae). There are two possible ways of rendering the chemical method of use for systematic purposes, viz. by macroscopic analysis and by micro-chemistry. The former is naturally only of value in connexion with the scientific side of systematic Botany, that is to say with questions of affinity, and not with the practical determination of plants, since it requires a large amount of material. Greshoff [2] entered on this line of research

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[1] Cf. Husemann and Hilger, Pflanzenstoffe, Berlin, 2 vols., 1882 and 1884. The following work gives the best information regarding micro-chemical reactions: Zimmermann, Bot. Mikrotechnik, Tübingen, 1892.

[2] Greshoff, Planten en plantenstoffen, Kon. Natuurk. Vereen. in Nederlandsch-Indië, n. 7, 1891.

and obtained successful results; it is to be hoped that these investigations, which were commenced at Buitenzorg, may be continued, since a tropical garden, supplied with plants belonging to all sections of the Natural System, is most suitable for this line of research. Battandier[1] and others followed Greshoff in this type of investigation. The second method is that of micro-chemical examination, which may be serviceable not only for the solution of scientific problems, but also in the determination of plants. It has been sufficiently explained above that the micro-chemical method, which alone forms a component part of the anatomical one, is still in a very rudimentary stage, and the reason has also been indicated. The first steps have, however, been taken. In diagnoses we can, in the first instance, make use of those substances which are deposited in special receptacles, or are excreted in a definite and visible form, and which can in some cases be determined by special chemical reactions. Thus mucilage, resins, oxalate of lime or crystalloids occur in many Natural Orders, whilst hesperidin is found in the Rutaceae and gypsum in certain species of *Capparis* and in other Capparideae; again, sphaero-crystalline deposits of diverse nature are met with in many plants, inulin in the Compositae, myrosin in the Cruciferae, Capparideae and Resedaceae, and so on. One must welcome the fact that Guignard's excellent work on myrosin has led other investigators to commence the study of the micro-chemistry of vegetable substances, and of the localization of the latter within the plant.

At the present time the employment of anatomical, as compared with micro-chemical, features stands on a much better basis. It is around the former that the anatomical method at present centres, leaf and axis being principally concerned. It has already been indicated at the beginning of the introduction, that the anatomical method is only a detailed and elaborated morphological method,—to use Radlkofer's expression, only an endomorphic as contrasted with an exomorphic one. For this reason, the experience acquired in the employment of external morphological characters is equally applicable to internal ones. Moreover, the correctness of this proposition has also been confirmed by the numerous investigations which have been undertaken along the new line of research, especially those dealing with the important question of the constancy of anatomical characters. These latter are no more capable than are the external ones of being brought into a definite system in accordance with their systematic importance. Both endomorphic and exomorphic characters have been shown to possess great systematic value in one group of affinity, though of small importance in another. Their systematic value simply depends on the length of time the characters in question have remained unaltered or uninfluenced by adaptation during the development of a plant-phylum. Hence the importance of examining the constancy of anatomical characters from species to species, from genus to genus, from order to order without preconceived ideas[2].

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[1] *Battandier, Caract. taxin. tirés de la chimie végét., Assoc. franç., Carthage, 1896, pt. ii, p. 440.* From this source most of the examples enumerated above are taken.

[2] Contrary to the foregoing views, Vesque, whose investigations have otherwise done so much for the development of the anatomical method, ascribes a definite degree of value to the different characters. It may be pointed out for the benefit of those who have occasion to refer to the important works of Vesque, that he separates the characters into such as are phyletic and quite independent of adaptation, and into those which are adaptive. He classifies the latter into those adapted in consequence of their relation to the animal world or to other plants, those adapted for the distribution of seeds and so on, and into such as are adapted to physical media. The latter alone constitute his epharmonic characters, which, according to him, are really constant for the species only. The remainder constitute his taxonomic features, which are characteristic of the larger groups. If an epharmonic character is common to the species of a large systematic group, it is described by Vesque as 'allure épharmonique.' This is intended to express the fact that an epharmonic character in the

The foregoing statements are not, however, meant to imply that the numerous investigations which have been carried out have not afforded certain criteria, enabling one to judge which anatomical characters are usually of most systematic value. For otherwise the statements laid down in this book, and in part merely based on preliminary investigations, would be of no great value.

Anatomical characters may be divided into two groups: such as have been acquired independently of external biological conditions (at an unknown period and from unknown causes), and such as can be interpreted as adaptations to climate and habitat, or, in other words, to illumination, dampness of soil and atmosphere, as also to animals, mechanical factors, to a twining habit, or to a parasitic or saprophytic mode of life. The characters of the first group, which may be described as phyletic or ancestral, usually possess greater systematic importance than those of the second group, which are very frequently characteristic of species only; to these latter, the term physiological or biological characters may be applied.

The more important phyletic characters are:—the differentiation of the stomatal apparatus and of the hairy covering; the structure of the various internal and external glands; the mode of excretion of oxalate of lime; the occurrence of cystoliths; certain anomalous structural features of the axis, among which intraxylary soft bast is the most important. These features are not always characteristic of large groups of plants. Secretory cavities or cells, though often constant throughout entire Orders, tribes, or at least genera, may occasionally occur in isolated species. A definite type of stomatal apparatus is found without exception throughout the Rubiaceae, but is only present in isolated members of the allied orders, Umbelliferae and Caprifoliaceae, and so on. One or more exceptions may not rarely be found in an Order, the remaining members of which are distinguished by a special phyletic character; thus *Drapetes* is exceptional among the Thymelaeaceae in possessing no intraxylary phloem. Such cases are not capable of explanation, for these exceptional members have to be included in the Order concerned on account of the rest of their distinctive characters. All these facts indicate that the value of an anatomical character cannot be definitely predicted.

The physiological or biological characters require a fuller discussion. Numerous physiological treatises have been published, dealing with the adaptability of anatomical structure to illumination [1], to the degree of moisture in the soil and in the air (i.e. to climate and habitat [2]), to mechanical factors, and so

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phyletic sense cannot characterize a larger group of affinity than the species, but may afford a serviceable feature for the determination of this group.

[1] Stahl, Einfl. der Lichtintens., Bot. Zeitg. 1880, p. 868 and Sonnig. u. schatt. Standort, Zeitschr. f. Naturw., Jena, 1883.—Hentig, Stell. d. Bl. etc., Bot. Centralbl. 1882, iv. p. 415.—Pick, Einfl. d. Lichtes auf d. Gest. u. Or. d. Ass.-Gew., Bot. Centralbl. 1882, iii, p. 400.—Johow, Bezieh. einig. Eigensch. der Laubbl. zu d. Standortsverh., Pringsheim Jahrb., Bd. xv, 1884, p. 282.—Haberlandt, Ber. deutsch. bot. Gesellsch. 1886, p. 206; see also Pringsheim Jahrb., Bd. xiii, 1881.—Dufour, Influence de la lumière, Ann. sc. nat., sér. 7, t. v, 1887, p. 311 and especially p. 355, and Journ. de bot. 1887, p. 177.—Eberdt, Pallisadenpar., Ber. deutsch. bot. Gesellsch. 1888, p. 360.—Warming, Oekol. Pflanzengeogr., Berlin, 1896, p. 19.—[Costantin, Les végét. et les milieux cosm., Paris (Alcan), 1898.]

[2] Czech, Stomata, Bot. Zeit. 1869, p. 820.—Tschirch, Anat. Bau d. Ass.-Org. zu Klima u. Standort, Linnaea, Bd. xliii, 1880–2, p. 138.—Areschoug, Einfl. des Klimas etc., Engler, Bot. Jahrb., Bd. ii, 1882, p. 511.—Johow, loc. cit.—Fleischer, Schutzeinricht. d. Pflanzenbl. vor Vertrockn., Ber. Realgymnas. Döbeln, 1885.—Volkens, Standort u. anat. Bau, Jahrb. Berlin. Gart., Bd. iii, 1885, p. 1.—Giltay, Nederl. kruidk. Archief 1886, p. 413.—Warming, Grönlands Vegetat., Engler, Bot. Jahrb., Bd. x, 1888, p. 364.—Burgerstein, Material. z. einer Monogr. d. Transpirat. ii, Verh. k. k. zool.-bot. Gesellsch. Wien 1889, especially pp. 412 and 454.—Göbel, Pflanzenbiol. Schild., especially Teil ii, Lief. 1, 1891.—Meigen, Engler, Bot. Jahrb., Bd. xviii, 1894, p. 394.—Reiche, Rio Maule, Engler. Bot. Jahrb., Bd. xxi, 1895, p. 38.—Stenström, Vork. ders. Art. in versch. Klimaten etc., Flora 1895, pp. 117 and 421.—Diels, Veg.-Biog. v. Neuseeland, Engler, Bot. Jahrb., Bd. xxii, 1896, p. 202.—Grevillius, Ins. Oeland, Engler, Bot. Jahrb., Bd. xxiii, 1896, p. 24.

on. Adaptive features have been recognized as such by various means:—by the examination of individuals of the same species from different habitats or by experimental treatment under definite conditions, differing from those of the natural habitat; by the study of a larger group of plants, undertaken in relation to the geographical area over which its members are distributed; and lastly by comparative investigation of the species of a plant-association (e.g. xerophytes[1], water-plants[2], Arctic plants[3], Alpine plants[4], halophytes[5] and evergreen plants[6]).

Strong illumination and the consequent increase of transpiration and assimilation occasion the development of palisade-tissue in the leaf. By the production of palisade two principles, which were discovered by Haberlandt, are fulfilled, viz. the increase of surface in the assimilatory tissue and a provision for conducting away the products of assimilation as rapidly as possible. Light of different degrees of intensity, acting as a stronger or weaker stimulus, is connected with the centric or bifacial structure of the leaf and the qualitative and quantitative differentiation of palisade and spongy tissue. Anthocyanin is sometimes present and represents a means of protection against light of too great intensity. Protection against desiccation, or, more correctly, against excessive transpiration, is provided for by arrangements of two kinds, viz. such as insure against loss of water and such as consist in the formation of special water-reservoirs. The following are arrangements of the first kind: development of papillae and of hairs; thickening of the walls of the epidermal cells, development of a thick cuticle, deposition of wax, resinous substances or incrustations of salt on the surface, infiltration of silica, calcium carbonate or oxalate-crystals in the epidermal walls; diminution of the number of stomata, or of their size, or of the size of their pores, occurrence of various arrangements in the guard-cells or subsidiary cells, by which the interchange of gases is impeded (e. g. the formation of excrescences on the guard-cells or of papillae on the adjacent cells, and so on), the more or less marked depression of the guard-cells below the level of the epidermis and the formation of an outer vestibule (chimney), often of considerable depth, above the stoma, restriction of the stomata to depressions of various types occurring on the lower side of the leaf, or on the surface of the stem, or on the upper side of the leaf, when the latter is adpressed to the stem; diminution of intercellular spaces; slight development of the vascular system; differentiation of palisade-tissue in the cortex of the stem, combined with reduction of leaf-surface (in plants with reduced foliage); salt as a constituent of the cell-sap; the development of ethereal oils serving to lower the diathermanous equivalent, and the differentiation of internal and external glands, which produce these substances. The following arrangements serve for the storage of water: enlargement of the epidermal cells, formation of hypoderm and transformation of different regions of the assimilatory tissue into aqueous elements; mucilaginous cells in the epidermis and ground-tissue; trichomes, which absorb or store up water; finally the formation of special storage-tracheides, which either arise through the modification of the terminal portions of veins or belong to the ground-tissue. All these structural features are biological characters of xerophytes, as also of halophytic and evergreen

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[1] Volkens, loc. cit. and Aegypt.-arab. Wüste, Berlin, 1887.—Warming, Oekolog. Pflanzengeogr., p. 177.

[2] Mer, Bull. Soc. bot. de France 1881, p. 87.—H. Schenck, Struktur-veränd. submers. veget. Landpfl., Ber. deutsch. bot. Gesellsch. 1884, p. 481 and cf. Anat. d. submers. Gew., Bibl. bot., Heft 1, 1886.—Constantin, Feuilles aquat., Ann. sc. nat., sér. 7, t. iii, 1886, p. 94 and especially p. 114.—Göbel, Pflanzenbiol. Schild., Teil ii, Lief. 2, 1893, p. 215.—Warming, Oekolog. Pflanzengeogr., p. 126.

[3] Boergesen, Anat. d. feuilles des pl. arct., Journ. d. bot. 1895, p. 1.

[4] Bonnier, Bull. Soc. bot. de France 1887, p. 467, and 1888, p. 436, Revue gén. de bot. 1890, p. 513, and Adapt. des pl. au climat alpin, Ann. sc. nat., sér. 7, t. xx, 1895, p. 217.—Leist, Einfl. d. alp. Standortes etc., Mitt. naturf. Gesellsch. Bern 1889.—Schimper, Schutzmittel d. Laubes etc., Monatsber. Berl. Akad. 1890, p. 1045.—Wagner, Biol. d. Alpenpfl., Sitz.-Ber. Wiener Akad., Bd. ci, 1892, p. 487.—Lazniewski, Beitr. z. Biol. d. Alpenpfl., Diss., München, 1896, and Flora, 1896.

[5] Schimper, loc. cit. and Indo-Malay. Strandfl., Jena, 1891.—Warming, Vesterhavskyst. marskegne, Vid. Meddelels. naturh. For. Kjöbenhavn 1890; Halofyt Studier, R. Danske Vid. Selsk. Skr. 1897, and Oekolog. Pflanzengeogr., p. 292.

[6] Schimper, loc. cit., and Lalanne, Feuilles persist., Act. Soc. Linn. de Bordeaux, sér. 5, t. iv, 1890.

plants. Alpine and arctic plants do not bear the impress of a definite type of structure, because their conditions of life are less uniform. A number of common characters, however, appertain to water-plants, which structurally form the opposite extreme to xerophytes, while shade-plants approach water-plants in structure. The effects of an aquatic mode of life are as follows. Its influence on the development of stomata is considerable; submerged leaves have few or no stomata, floating leaves as a rule produce them on the upper side only, whilst water-leaves of land plants usually have more on the upper than on the lower surface. The epidermal cells of water-plants have thin walls, the outline of the lateral walls being usually straight; the cells contain chlorophyll and have a weakly developed cuticle. The hairy covering is reduced, and, when trichomes are present, they commonly excrete mucilage. The palisade-tissue is little developed or wanting, while the system of intercellular spaces is more elaborate; the assimilatory parenchyma is poor in chlorophyll. Except in floating leaves the mechanical tissue (sclerenchyma and collenchyma) is reduced and the same is the case with the wood and bast of the vascular bundles. Finally, the development of aerenchyma in place of cork is also connected with the aquatic habitat. We have still to turn our attention to those anatomical features, which may be interpreted as mechanical adaptations. Among these are: the differentiation of a rigid cylindrical mass of xylem in woody plants; the complicated structure of the axis in certain lianes [1], in which the xylem-mass resembles a cable and is thus adapted to the requirements of tension and rigidity as well as torsion; the slight differentiation of the mechanical tissues (already referred to) in water-plants and likewise [2] in the subterranean parts of plants; the occurrence of spicular cells of various shapes in the thick leaves of xerophytes; the nature of the lateral walls of the epidermal cells [3]; and perhaps also the vertical transcurrence of the smaller veins of the leaf by means of a special tissue accompanying them. Lastly, it remains to call attention to the reduction in the number of stomata, in the development of the assimilatory tissue and in its chlorophyll-contents, which is the result of parasitism.

All these adaptations, however, must not be supposed to be quite general. For, if that were so, all plants which were subjected to the same conditions would possess the same biological structural features, even if they belonged to the most widely separated systematic groups. This is sometimes the case, and specially good examples are to be found amongst water-plants; a classic illustration of this is afforded by the structure of the leaves of *Nymphaea* and *Limnanthemum*, which resemble one another externally and agree not only in the mode of differentiation of their mesophyll, but also in the possession of spicular cells developed as internal hairs. But this is by no means always the case. *Experience shows that one species reacts in one way and another species* in a different way under the action of the same stimulus, but that the reaction is often of the same kind in plants belonging to the same phylum. Thus one species protects itself against desiccation solely by means of mucilage-receptacles, another by the development of hypodermal aqueous tissue, a third by enlargement of the epidermal cells, a fourth by means of storage-tracheides, others again by combinations of two or more of these structural features, and so on. In addition to this, climate and habitat do not impress any one definite type of anatomical structure, to be correlated with these factors, upon all the species of a certain geographical area; this is shown by the examples given by Reiche, Volkens, and others. Areschoug has further quoted instances, such as the leaf-structure of *Rosmarinus officinalis* and *Ilex Aquifolium*, which show that the internal structure does not always harmonize in every respect with the climatic conditions. And finally, it may be well to mention the fact that the differentiation of the mesophyll, which may be strongly influenced by the intensity of illumination, is in many cases already accomplished in the young

[1] See H. Schenck, Anat. d. Lianen, 1893, p. 25, and the older literature considered there.

[2] Costantin, Bull. Soc. bot. de France 1883, p. 230, and Ann. sc. nat., sér. 6, t. xvi, 1883, p. 1. —Nilsson, Dikotyla jordstammar, Acta univ. Lund., vol. xxi, 1885–6.

[3] Vesque, Compt. rend., t. xcvii, 1883, p. 201.

leaves, when still enclosed in the bud, and in the cotyledons of the dormant embryo in the seed. From all that has been said it follows that the species possesses a definite plasticity, which may vary in degree and direction in individual species. Where we find a discrepancy between structure and external conditions, we must assume that the discordant characters have been inherited from a previous generation living under different conditions [1]. This view is supported by the results of physiological researches, in which it has again and again been emphatically shown, that the anatomical structure is the product of two factors, adaptation and heredity. The second factor, which sometimes becomes more noticeable than the first, allows us to employ biological structural features to a very considerable extent for systematic purposes.

Biological characters serve primarily for the diagnosis of species. Within the same group of affinity they are often identical in all those forms in which they appear, while at times they may be constant for groups of allied species, for genera, or for small Orders. The last mentioned case may occasionally apply even to those characters, which respond most readily to external influences, such as the structure of the mesophyll (e.g. in the Hamamelideae). Biological characters may be divided into those which differ qualitatively, and those which differ quantitatively; of these the former have the greater systematic value. Thus the development of aqueous tissue in the leaf as hypoderm or otherwise is of more importance than the number of layers of hypoderm present, and similarly the nature of the markings of the cuticle is of greater value than their degree of prominence, and so on. However, the quantitative characters are also important for taxonomic purposes if they are employed with sufficient caution, i.e. after their constancy has been tested and if they are used to supplement other qualitative anatomical or exomorphic characters.

It is impossible to exaggerate the importance of studying the constancy of anatomical characters within a species. Abundant material from different habitats is generally at the disposal of systematists for this purpose. In order to solve the problem of the degree of variation of anatomical structure in the same species, we may in the following summarize those changes in anatomical structure which have been determined by different authors [2] by comparing specimens of the same species from different habitats or by cultivating certain species under altered conditions.

The epidermal cells of specimens from dry localities and from the Mediterranean region and those of sun-leaves have lateral walls, which are straight or less strongly undulated than is normal. Similarly the epidermal cells of the land-form of *Polygonum amphibium* are polygonal, whilst those of the water-form are provided with undulated lateral walls. The epidermal cells are of small size in specimens from dry habitats (Volkens), but have large dimensions (in all three directions of space)

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[1] According to Vesque and Areschoug the leaves of *Nelumbium*, although not floating, bear stomata on the upper side only, just like floating leaves. This fact favours the view that *Nelumbium* is derived from an ancestral form, possessing floating leaves.

[2] Literature: Lewakoffski, Einfl. d. Wassers etc. u. Einfl. d. Mediums etc., Gelehrte Schr. d. Univ. Kasan 1873, Russian, Abstract in Just 1873, p. 594.—Duval Jouve, Ann. sc. nat., sér. 6, t. i, 1875, p. 343.—Boehm, in Bot. Zeit. 1879, p. 254.—Haberlandt, loc. cit., 1881 and 1886.—Vesque et Viet, Infl. du milieu, Ann. sc. nat., sér. 6, t. xii, 1881, p. 167.—Pick, loc. cit., 1882.—Costantin, loc. cit., 1883.—Stahl, loc. cit., 1883.—Vesque, Causes et lim. des var. de structure etc., Ann. agron., t. ix, 1883, p. 481.—Heinricher, Isol. Blattbau, Pringsheim Jahrb., Bd. xv, 1884, p. 502.—H. Schenck, loc. cit., 1884.—Volkens, loc. cit., 1885.—Nilsson, loc. cit., 1885–6.—Kohl, Transpir. d. Pfl., Braunschweig, 1886.—Dufour, loc. cit., 1887.—Leist, loc. cit., 1889.—Wieler, Anat. u. Ausbild. v. Libriformf. in Abh. v. Suss. Verh., Bot. Zeit. 1889, p. 517.—Lésage, Rech. exp. sur les modif. des feuilles chez les pl. marit., Revue gén. de bot. 1890, p. 55.—Bonnier, loc. cit., 1895.—Russell, Infl. du climat méd., Ann. sc. nat., sér. 8, t. i, 1895, p. 322; see also Compt. rend. 1892 and 1895 and Assoc. franç. Caen 1884.—Stenström, loc. cit., 1895.—Grevillius, loc. cit., 1896.—Lazniewski, loc. cit., 1896.

in sun-leaves and in specimens from the Mediterranean region. Moreover, sun-leaves and plants from dry Alpine or Mediterranean habitats are commonly distinguished by a thick cuticle with strongly developed markings and by thick epidermal cell-walls, whilst in the water-forms of a species the corresponding features are progressively less developed than in the land-form. Reduction of papillae on the upper side of the leaf has been demonstrated (Leist) in specimens from a low-lying habitat as contrasted with those of a higher Alpine habitat; the papillae have been shown to be more strongly developed in specimens from dry habitats. The water-form of *Polygonum amphibium* is destitute of the mucilaginous epidermal cells, which occur in the land-form (Volkens); similarly according to Lazniewski, *Salix retusa* and *Daphne striata*, when cultivated in moist air, produce no mucilaginous epidermal cells. In branches remaining beneath the soil, a suberization of the epidermis ensues (Costantin). In the case of stomata the environment has been shown to affect their numbers only; thus an increase in number occurs in sun-leaves and in specimens from Alpine and Mediterranean habitats, whilst they become more numerous on the upper side of the leaf in specimens from damp habitats and in the water-form of *Cardamine pratensis* (H. Schenck). Reduction of the hypoderm has been demonstrated by Stahl in the shade-leaves of *Ficus stipulata* and *Ilex Aquifolium*, hypoderm-formation being restricted to the neighbourhood of the larger veins of the leaf in the second example; similarly the number of epidermal cells divided by horizontal walls is less in the shade-leaves than in the sun-leaves of *Tradescantia zebrina*. The development of hairs is favoured by cultivation in dry air, which influences both their number and length; in water-forms the trichomes of the corresponding land-forms are often entirely suppressed. In the structure of the mesophyll the development of palisade-tissue is favoured in sun-leaves and in specimens from Alpine (according to Bonnier) or maritime localities, the number of layers and the length of the cells being increased, whilst reduction of the intercellular system is generally associated with this change. The reverse occurs in specimens grown in moist cultures, in water-forms, in shade-leaves and sometimes (according to Leist) in Alpine plants. How far adaptation may be carried in this direction in the same species is illustrated according to Stahl by the beech, the shade-leaves of which have typical bifacial structure, whilst the sun-leaves are subcentric, and by similar examples, described by Pick and Heinricher, according to whom the lower and upper leaves of *Cirsium canum* and of certain species of *Centaurea* exhibit analogous differences. The primary cortical parenchyma is strongly developed and dense in plants cultivated in dry air; it is more extensive and lacunar in the water-form of a species than in the land-form. The vascular system attains a greater development than usual in specimens cultivated in dry air, in sun-leaves, and in the plants of the Mediterranean region, the vessels being larger. The water-forms as compared with the land-forms of the same species have the conducting tissue weakly developed, and this also applies to subterranean branches. The extent to which this modification may be carried within the same species is shown by Boehm's experiment with cuttings of *Salix* grown under water, in which no vessels were produced. The mechanical system (collenchyma, sclerenchyma, bast- and wood-fibres) attains a greater development in sun-leaves and in specimens from dry habitats, whilst these tissues are reduced in plants cultivated in moist air and in the case of water-forms, as well as in subterranean branches. In the axis of *Urtica dioica* Wieler succeeded in producing a decrease in the amount of thin-walled wood-parenchyma and a greater development and differentiation of wood-fibres by diminishing the water-supply, whilst in the axes of *Quercus* and *Robinia* a reduction in the number of wood-fibres followed a marked increase of the water-supply. In the same way Duval-Jouve describes a well-marked change in the differentiation of the hypodermal sclerenchyma in the leaves of various grasses according to the habitat. Enlargement of the secretory canals and increased amount of oxalate of lime have been recorded in the case of sun-leaves; the former feature has also been found in Alpine and Mediterranean specimens of certain species.

From the preceding statements it is clear that the variations in the anatomical features of the same species are essentially a matter of degree, depending on the quantitative development of biological characters. It is probable that this type of variability never exceeds certain fixed limits, as experience has shown. Epidermal cells of very large and of very small size have in no case been found on the corresponding leaf-surfaces of different individuals of the

same species, nor has the epidermis been observed to possess extremely strongly undulated lateral walls and such as are quite straight in corresponding positions. No case has been recorded of leaves of the same species bearing stomata in exceptionally large numbers on the upper side in some individuals, whilst there were none on this surface in others. Similarly, typical centric and typical bifacial leaf-structure is hardly to be found in the same species, of course, with the exception of those with dimorphic leaves, such as *Eucalypti*, in which the different types of anatomical structure are inherited together with the form and position of the leaf; nor should we expect to find a very strong annular sheath of sclerenchyma around the vascular bundles of the veins, if in other individuals of the same species sclerenchyma was entirely wanting. The most striking examples, inasmuch as they are qualitative, among the structural variations mentioned above, are the total suppression of mucilaginous epidermal cells in a few plants (Lazniewski) and the absence of mucilage-cells in the water-form of *Polygonum amphibium*. A similar example is afforded by the spicular cells which occur in the leaf of the tea-plant and have been proved to be entirely absent in some cases. The absence of mucilage-cells in the water-leaves of an amphibious species is not any more surprising than the last instance; it is quite easy to imagine that a certain plasticity may have developed in this class of plants in the course of time, for the case is analogous to that of the dimorphic leaves of *Eucalyptus*. As regards the exceptions to the normal structure in the leaf of the tea-plant it may be remarked that species have been proved to differ from one another in their degree of plasticity, which tends to be specially marked in species which, like the tea-plant, have been under cultivation for a long period. Concerning Lazniewski's experiment and those of Boehm and Wieler referred to above, it seems probable that the species never, or at any rate, extremely rarely, exists in nature under the conditions to which it was subjected in these experiments; the changes produced must therefore be regarded as pathological. Before leaving this subject it may perhaps be advisable to point out to those undertaking experiments on the variability of the anatomical structure within a species, that they should experiment with wild and not with the cultivated plants of our gardens and greenhouses, which may possibly have been under cultivation for many generations and may differ from wild plants in their degree of plasticity.

We are approaching the conclusion of this introduction, and I return once more to the question propounded in the preface, viz. whether all that was to be expected from the adoption of the anatomical method has been fulfilled or to what extent this fulfilment has been realized. The answer is in every respect favourable and the results obtained will only disappoint those who imagined that an entirely new era had begun for systematic Botany, with the introduction of the anatomical method, and who believed that the time had come at last for discarding the present classification, which, according to their views, was founded on a one-sided basis—that of the characters of the flower and fruit. No new system is created by the aid of the new method; it has rather become apparent that the classification based on external morphological characters, especially on floral features, and elaborated with great industry and skill, on the whole stands the test of the new method. The system created by the older taxonomic botanists is in its broad outlines a natural one, in so far, that is, as one can speak of a natural system at all without having investigated the palaeontological history. There can be no question of actually substituting anatomical characters for external features; we are only concerned with the employment of endomorphic in conjunction with exomorphic characters. The anatomical method is only an auxiliary one, although it is of great importance. Properly employed, i.e. when sufficient attention is also paid to external morphological features, it is of the greatest value both as a means of confirmation of results

already obtained and for the further elaboration of the Natural System. It provides a new series of distinctive features for the various groups of affinity, from the Order down to the species; these features especially afford excellent and much needed diagnostic characters for species and are thus of the utmost value to systematists. There are very few good species which do not present some distinguishing anatomical feature. Anatomical characters sometimes lend support to the results obtained by the use of external morphology, i.e. when they coincide with the external characters. Frequently, however, they disclose new points of view regarding affinities and thus serve to improve and complete the Natural System. Anatomical characters are often preferable for the determination and delimitation of a systematic group, since they are more precise than external morphological characters and possess the further advantage, that they necessitate detailed observation and prevent a superficial treatment and too hurried decision. Specific anatomical characters have been made use of as a means of recognizing hybrids [1], and it may be mentioned in passing, that they are also of value to cultivators, since they generally elucidate the habitat and climate wherein the species thrives. But anatomical characters come to be of special importance, when the necessity arises for determining a plant in an imperfect condition (as happens especially frequently in dioecious species) or for determining one provided with fruits alone or sterile. Although it is impossible to point out one or more prominent characters for every Natural Order, and we are not able to construct an efficient table for the determination of the individual Orders by their anatomical characters (a task, however, which proves very difficult also in the case of external morphological features), yet we have in many cases advanced far enough to be able to undertake the solution of the problems indicated above. The extent of this advance is probably best shown by mentioning that for the future any systematist, who is conversant with the new method, will, when determining a plant (even when the latter bears flowers), first prepare sections of the leaf and axis, with the purpose of seeing whether the structure does not afford some useful data in confirmation of the inferences deduced from the habit, regarding the Order to which the plant belongs; and this will be done before proceeding to a floral analysis, which is often laborious and may in some cases damage the material. A task, similar to that mentioned above, often presents itself in the course of the preparation of a monograph of an Order or genus, when it becomes necessary to investigate old and frequently very fragmentary material and to correct the mistakes which have been associated with the latter; for this purpose also the employment of anatomical characters is in many cases the only sure method towards the attainment of this end.

It is necessary, however, to give an emphatic warning against any over-rating of anatomical characters, for examples of errors in this respect are already to be found in the literature. In his treatise on the Thymelaeaceae, Gilg rightly takes exception to the manner in which Van Tieghem uses anatomical features in this Order for generic diagnosis and for the establishment of new genera without having carefully tested the constancy of these characters; in other cases, however, Van Tieghem has contributed greatly to the anatomical method by his many excellent works. In like manner, Pierre unwarrantably

[1] Literature: Wettstein, Sitz.-Ber. Wiener Akad., Bd. xcvi, Abt. 1, 1887, p. 312; Brandza, Compt. rend., t. cxi, 1890, p. 317, Revue de bot. 1890, pp. 301 and 433 and Journ. de bot. 1890; Macfarlane, Transact. Royal Society of Edinburgh, vol. xxxvii, part i, 1892, p. (203); Wunderlich, *Cirsium*-Bast., Diss., Erlangen, 1895; Hartwich, Arch. sc. phys. et nat., 4e pér., t. ii, 1896, p. 428. According to these works, which deal with the structure of the axis and leaf and also with the features presented by the crystals, hybrids either possess the structural peculiarities of both parents side by side, or have an intermediate structure; the former may sometimes apply to one organ, the second condition to another organ of the same hybrid.

overrates a single character, when he (Bull. Soc. bot. Linn. de Paris, 1897, p. 1225) divides the Dicotyledons into Monoxylées, Dixylées and Trixylées according to the number of vascular bundles passing out into the petiole, neglecting the fact that the structural features of the petiole have, for the most part, proved to be of value for specific diagnosis only. The value of an anatomical character must be accurately determined in each individual case, since it may differ in different groups of affinity. Further, when anatomical features are employed, their physiological function must be taken into account, for a consideration of the latter will often enable one to come to a conclusion as to their value. Finally, in the solution of systematic problems, the exomorphic must invariably be taken into due consideration together with the endomorphic characters.

To those who are unacquainted with the anatomical method, the results enumerated above may perhaps appear somewhat meagre in proportion to the large amount of labour and trouble which the method involves; to the initiated, however, they are considerable. And even though the attainment of a Natural System has only been slightly advanced by the new method, we must grasp and make use of every means which tends towards this end. Each era has its own scientific methods, and these are connected with the development of science as a whole. Thus systematic Botany has already received much assistance from a whole series of methods besides that of comparative morphology; to use Radlkofer's words, we may describe these different methods respectively as the diagrammatic, the developmental, the teratological, the geographical, the palaeontological, the physiological, the chemical and the experimental; and systematists now possess the anatomical method also. This should be borne in mind by those to whom the new method does not afford sufficient scope for their speculative turn of mind, and also by those who wish to urge systematic Botany towards its goal. With the advance of time newer methods will undoubtedly arise for the use of systematists; they will take their position beside the older ones and will yield new results. With the further development of chemistry, the micro-chemical method will play a greater part in systematic Botany than at the present time. And should it become possible at some future date to obtain information by microscopical means regarding the resemblances and differences in the molecular structure of the nuclei and protoplasm in the cells of the growing-point and in the ova of different species, or, in other words, to discover the character of the idioplasm of a species, this also would become part of the anatomical method.

ANATOMICAL CHARACTERS OF THE DICOTYLEDONOUS ORDERS

RANUNCULACEAE.

1. REVIEW OF THE ANATOMICAL FEATURES. The most important anatomical characters are as follows. The appearance of the vascular bundles in transverse section is characteristic for most members of the Order, the xylem having the form of a V (Fig. 1, *C*) and partly enclosing the soft bast with its arms. In the woody and in many of the herbaceous species there is a tendency to the formation of a composite and continuous ring of sclerenchyma in the pericycle. The perforations of the vessels are almost always simple; *Paeonia* stands alone in possessing exclusively scalariform perforations. Where wood-prosenchyma occurs, it is simply-pitted. The origin of the cork is internal in the cases observed. The stomata have no special subsidiary cells. The hairy covering consists of clothing hairs and glandular hairs. The former (Fig. 1, *D–E*) are mostly unicellular, thickened on all sides or on one side, or thin-walled; simple uniseriate trichomes are found in *Thalictrum*. The glandular hairs (Fig. 1, *F–J*) are always unicellular; they secrete either (rarely) ethereal oil or mucilage, or (more frequently) serve as hydathodes (water-glands). Oxalate of lime is not often present. In *Paeonia* it occurs in the form of clustered crystals, in other genera in the form of fairly small, rarely rather large crystals of the tetragonal system. As special anatomical features in the Order, the following should be mentioned: the arm-palisade-cells (Fig. 1, *A–B*) in the palisade-tissue of the leaf in species of *Aconitum, Anemone, Caltha, Paeonia*, and *Trollius*; the water-pores and mucilage-secreting structures on the leaf-teeth of certain members of the Order; the anomalous stem-structure in some cases, namely the arrangement of the vascular bundles in several circles in species of *Actaea, Cimicifuga*, and *Thalictrum*, and the occurrence of medullary vascular bundles in *Anemone japonica*, &c.; finally the structure of the stem of *Clematis* and probably also of *Naravelia*, belonging to what is called the *Aristolochia*-type.

2. STRUCTURE OF THE LEAF. The following description is based chiefly on the statements of Vesque, taking the remaining literature into consideration.

The following points may be noted with regard to the **epidermis** of the leaf. The epidermal cells of the lower side of the leaf almost always possess strongly undulated lateral walls, which in the angles of the crenations sometimes project in the form of ridges and end in knob-like swellings. The lateral walls of the epidermal cells on the upper side of the leaf are mostly not undulated. With regard to the lateral walls of the epidermal cells it is also worthy of note, that, according to Askenasy, they are straight in the laciniae of the normally submerged forms of *Ranunculus aquatilis* and *R. divaricatus*, while in the land-forms of the same species they are undulated, and that sometimes (*R. lanuginosus* and *R. Aleae*), according to Nestler, there is a localized separation of the lateral walls, producing chambers ('Höfen') of varied size between the epidermal cells. Markings of the cuticle in the form of ridges have been observed in the leaf of *Ranunculus Cymbalaria* (upper side), of species of *Helleborus* (upper side) and of *Clematis Vitalba* (lower side). In *Clematis balearica*, Rich., and *C. cirrhosa*, L.,

and in these species only, Nestler locally met with a peculiar penetration of the cuticle between the lateral walls of adjacent epidermal cells in the form of a wedge-shaped process. The dull surface of the leaf in species of *Aquilegia* and *Thalictrum* is caused by slight papillose protuberances of the central parts of the epidermal cells; a similar formation of papillae is found also on the veins of the leaf in the species of *Helleborus*. In certain cases (in *Caltha palustris*, *Ranunculus Ficaria*, and in *Batrachium*) chlorophyll occurs in the epidermal cells.

The **stomata** have no special subsidiary cells, but are surrounded in an irregular manner by a rather large number of ordinary epidermal cells. With regard to the development, Vesque has determined that in *Eranthis* the mother-cell of the guard-cells is cut off by the first division, and is thus identical with the initial cell. Usually (*Paeonia*; *Atragene*; *Xanthorhiza*; *Naravelia*; *Helleborus*; *Thalictrum* pro parte, namely with the exception of *T. tuberosum*, L.; *Clematis* pro parte, namely with the exception of *C. Flammula*, L., *C. orientalis*, L., and *C. Oweniae*, Harv.) the stomata are found only on the lower side of the leaf. More rarely they occur on the upper side also, and in that case either in small numbers (*Hepatica triloba*, *Ranunculus acer*) or abundantly (*Anemone Pulsatilla*, *Ranunculus Flammula*, *R. Lingua*, and *R. sylvaticus*), in the latter case sometimes (*Ranunculus alpestris* and *R. sceleratus*) even exceeding the stomata of the lower side of the leaf in number. In the floating leaves of *Batrachium* the stomata are naturally found only on the upper side; similarly in *Caltha dioneaefolia*, Hook. fil. (which is an extremely interesting plant, and will consequently be more fully discussed below) and in its allies it is only the upper surface of the leaf that bears stomata. Stomata are absent in the water-leaves of those species of *Ranunculus* which belong to the section *Batrachium*.

The **leaf-structure** is almost always bifacial, rarely (*Delphinium Consolida*) centric. In *Pityrosperma acerinum* and in *Batrachium* the mesophyll shows no differentiation into palisade and spongy tissue. With regard to the palisade-tissue, it should be mentioned that in certain cases the arm-palisade-cells of Haberlandt occur (Fig. 1, *A–B*). Haberlandt states that these are found in *Aconitum Napellus*, *A. dissectum*, *Caltha palustris*, *Clematis integrifolia*, *Paeonia corallina*, *P. tenuifolia*, *Trollius europaeus*, and a special form of them (H-shaped arm-palisade-cells) in *Anemone sylvestris*; on the other hand, in numerous species of the genera *Anemone*, *Aquilegia*, *Delphinium*, *Eranthis*, *Helleborus*, and *Ranunculus* (including *Ficaria*), Haberlandt did not meet with palisade-cells of the form in question. The small veins of the leaf are embedded in the mesophyll; the rather larger ones extend, by means of the thin-walled, somewhat collenchymatous tissue accompanying them, as far as the epidermis on both sides. In the still larger veins and in the midrib, bast-fibres are usually present on both sides, or only on the lower side, of the vascular bundle.

Further, the occurrence of water-pores on the crenate teeth of the leaf is worth mentioning. According to Strasburger they occur singly in *Aconitum*, *Delphinium* and *Eranthis*, in pairs in *Helleborus niger*, and several together in *Ranunculus lanuginosus*; according to Nestler they are quite generally present in the species of *Helleborus* and *Ranunculus* (also of *Batrachium*), but are absent in *Paeonia* and usually also in *Clematis* (exceptions:—*C. dioica*, L., var. *brasiliensis*, Eichl., and *C. cirrhosa*, L.). Glandular leaf-teeth secreting mucilage are described by Reinke for *Caltha palustris*, *Helleborus intermedius*, and *Ranunculus repens*.

Oxalate of lime is not frequently present in the Order; however, it is by no means absent. In *Paeonia* it occurs in the form of clustered crystals in the parenchyma of the leaf, root, &c. Nestler has observed rather small crystals, which belong to the tetragonal system, in numerous species of *Ranunculus* (e.g. *R. aconitifolius*, where they occur in almost every cell of the lower epidermis of the leaf, *R. alpestris*, *R. arvensis*, &c.), as well as in *Helleborus Kochii*, Schiffn.,

and larger solitary tetragonal crystals in the ground-tissue of the petiole of *Ranunculus asiaticus*. The large rhombohedra of the oblique (klinorhombic) system, so widely distributed in other Orders, have not been met with in any of the Ranunculaceae.

The **hairy covering** consists of clothing hairs and glandular hairs. The clothing hairs (Fig. 1, *D–E*) are mostly unicellular, of varied length, with blunt or pointed tips, thickened only on one side (species of *Clematis*), or thick-walled on all sides and in that case narrow-lumened (*Anemone, Ranunculus*), or very thin-walled and ribbon-like in appearance (*Actaea, Cimicifuga, Pityrosperma*). Occasionally the base of the hair is bulbously swollen and the neighbouring epidermal cells project upwards like a pedestal; further, twin-trichomes are produced in the grooves of the upper side of the leaf (especially frequently in

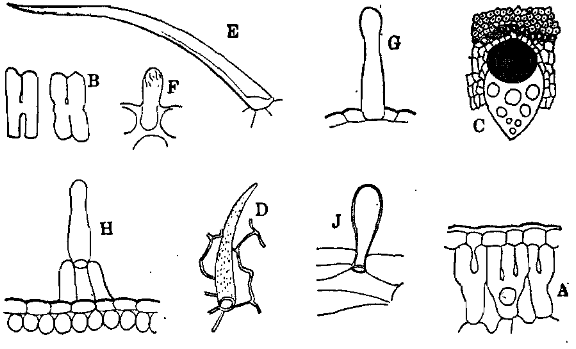

FIG. 1. A–B, Arm-palisade-parenchyma from the leaf of *Paeonia tenuifolia* (A) and of *Anemone sylvestris* (B). C, Diagrammatic transverse section of a vascular bundle and the neighbouring tissue in the petiole of *Thalictrum foetidum*, L. D, Clothing hair of *Aconitum autumnale*. E, Trichome of *Clematis Savatieri*, thickened on one side. F–J, Glandular hairs: F, *Eranthis hyemalis*; G–H, *Thalictrum foetidum*; J, *Ranunculus acer*. A–B after Haberlandt, D–F after Vesque, J after Nestler, the remainder original.

Ranunculus repens, more rarely in *R. aquatilis*) by the juxtaposition of the trichomes in question. The surface of the unicellular clothing hairs is either smooth or punctate or striated. Simple uniseriate clothing hairs consisting of a few long cells have been observed only in *Thalictrum* (*T. angustifolium*, Jacq., *T. foetidum*, L., and *T. purpurascens*, L.), and in some cases occur side by side with unicellular hairs. The small unicellular trichomes, which have been observed in species of *Ranunculus, Caltha, Clematis* (including *Atragene*), *Helleborus, Thalictrum*, and also in *Eranthis*, must be classed as glandular hairs. According to Nestler and Schilling the glandular hairs of the *Ranunculi* (*R. acer*, *R. fluitans, R. Friesianus, R. lanuginosus, R. bulbosus, R. umbrosus*, see Fig. 1, J), and of *Caltha palustris*, L., are unicellular, club-shaped and thin-walled, and occur in the grooves of the veins on the upper side of the leaf, and also on the leaf-sheaths. Usually no secretion is formed in them; they have mostly colourless contents, and probably serve for the absorption of water. The only exception to this is afforded by the glandular hairs of the two water-plants

cited (*Ranunculus fluitans* and *Caltha palustris*), which, according to Schilling, excrete mucilage, as do the trichomes of many other water-plants. According to Vesque and Nestler the species of *Helleborus* possess trichomes identical with those of *Ranunculus* and *Caltha*. *Thalictrum* has true glandular hairs (Fig. 1, *G–H*), as Lecoyer was the first to point out. These likewise are unicellular and thin-walled, but produce an oily secretion. In *Thalictrum foetidum* I found both sac-like glandular hairs, similar to those of *Ranunculus* and *Helleborus*, and also others, which exhibit a more or less distinct differentiation into a longish stalk, somewhat inflated in its lower part, and a spherical head; both forms are sometimes found on a conical pedestal formed by the upgrowth of several epidermal cells or of short rows of these cells. The trichomes of *Eranthis hyemalis* figured by Vesque, which are short and broad, rod-shaped and unicellular, may no doubt also be included among the glandular hairs (in the wider sense adopted here).

Internal glands are not present in the Ranunculaceae. Oily contents, however, characterize the parenchymatous cells in the root and rhizome of *Eranthis* and *Helleborus*, and further, a yellow coloration caused by berberine is to be seen in the perennial parts and the roots of *Coptis*, *Hydrastis*, *Xanthorhiza* and some species of *Thalictrum*.

The structure of the **petiole** has been investigated especially by Plitt and Petit in species of *Aconitum*, *Actaea*, *Adonis*, *Anemone*, *Aquilegia*, *Caltha*, *Clematis*, *Delphinium*, *Helleborus*, *Nigella*, *Paeonia*, *Ranunculus*, *Thalictrum*, and *Trollius*. Without going into details, the following points only need be mentioned here: (1) the outline of the transverse section of the petiole in the characteristic region (='caractéristique,' i.e. at the upper end of the petiole), and the details of differentiation of the fibro-vascular system in this region, have proved to be of use for more special diagnosis; (2) the vascular bundles present in this region are almost always separate (with the single known exception of *Clematis Flammula*, where the xylem of the vascular bundles is fused into a ring), their number varying within wide limits; they are either arranged in an arc, or in a circle, and are of equal size or alternately large and small; (3) in most cases the V-shape of the xylem in transverse section (cf. Fig. 1, *C*) is clearly marked; (4) sometimes (*Actaea*, *Anemone elegans*) medullary vascular bundles are present inside the ring of bundles.

Finally, the leaf-structure of *Caltha dioneaefolia*, Hook. fil., deserves a short description. This is an interesting little plant belonging to the antarctic Flora of Magellan. Its leaves with their marginal teeth, and their two appendages, folded back towards the surface of the leaf, to some extent recall the leaves of *Dionaea muscipula* (the American Fly-trap). Behrens, without any detailed investigation of his own, has drawn the conclusion that the *Caltha* in question is a new insectivorous plant. Closer examination of the leaf does not afford the slightest support to this view, as Goebel has already pointed out. The leaf is bifacial in structure; weakly developed palisade-tissue is found on the upper side. The stomata are likewise situated exclusively on the upper side (inner side); external as also internal glands are completely absent. The statement, 'foliorum lamina . . . superne . . . papillosa' in the 'Flora antarctica,' which led Behrens to assume that the inner side of the lamina was quite densely beset with sticky papillose hairs, is incorrect and to be attributed to the prominent appearance of the stomata on examination with a lens. Possibly, when the habitat of the plant becomes submerged the peculiar leaf-apparatus in this species serves to prevent the upper surface of the leaf with its stomata from being wetted, a annd to form air-chamber. According to Goebel and Diels, the same leaf-appendages and similar restriction of the stomata to the upper side of the leaf occur also in other antarctic species of *Caltha*, belonging to the section *Psychrophila*, e.g. *C. sagittata*, Cav., *C. andicola*, Gay, and *C. Novae Zelandiae*, Hook. f.

3. Structure of the Axis. Only a few representatives of the Order are woody plants, namely species of the genera *Clematis* and *Naravelia*. In these genera the structure of the axis, as is to be expected, possesses definite pecu-

liarities as compared with that of their allies, and will be discussed separately below. But first, the features common to the structure of the axis in the Ranunculaceae may be pointed out. The vascular bundles in the transverse section of the stem almost always show the same conformation, even in *Clematis* and *Naravelia*. The xylem of each bundle has the form of a V; it projects as an acute wedge towards the pith, is strongly broadened towards the outer side and finally divides into two arms, which partially enclose the soft bast while the latter is further often bounded externally by a crescent of hard bast the ends of which enter into connexion with the arms of the xylem. As is well known, the form of vascular bundle just described is present in many Monocotyledons, but is rare in Dicotyledonous plants. According to Vesque, an exception is afforded for example by *Paeonia*, the xylem of the vascular bundle in this plant being flattened on the outer side. It must also be mentioned that wherever wood-prosenchyma occurs, it is provided with simple pits on its walls, and that hitherto only simple perforations have been observed in the vessels of both the woody and the herbaceous genera, with the single exception of *Paeonia*, in which Chalon and Alb. Meyer have demonstrated the exclusive occurrence of scalariform perforations with few bars.

Both the **woody genera**, *Clematis* and *Naravelia*, are primarily distinguished as regards the structure of the axis by conforming to the type of the Aristolochiaceae. The primary medullary rays are broad, and do not become closed by interfascicular wood during secondary thickening, form continuous plates, which are somewhat broadened towards the exterior, and divide the mass of wood into a corresponding number of longitudinal segments. The secondary medullary rays are likewise broad, and behave in the same way as the primary rays. The vascular bundles are separated clearly from one another by the broad primary medullary rays, and the vascular bundles themselves are split up in a fan-like manner by the secondary rays. The number of the (primary) vascular bundles amounts to twelve in *Clematis Vitalba* and *C. campestris*, but is greater in *C. dioica*, L. (twenty or twenty-four). Of the twelve vascular bundles present in the young internode of *C. Vitalba*, six arise earlier, and the remaining six (alternating with the former) somewhat later. Owing to the fact that the latter six bundles, the so-called intermediate bundles, sometimes originate late and nearer the pith than the others, and produce a smaller quantity of xylem, a lobed xylem-mass is produced, which is similar to that of certain Bignoniaceae, characterized by the possession of phloem-wedges; this has been met with by Krasser in branches of *Clematis Vitalba* growing in the neighbourhood of Vienna. In the node the vascular bundles of the young stem anastomose freely, and so do the xylem-plates of the old stem; in addition, the medullary rays in the internode are traversed by solitary oblique groups of tracheides. The following facts are known with regard to the nature of the wood, cortex, and pith in the woody species. The cells of the medullary rays have lignified walls in *Clematis Vitalba*, unlignified in *C. dioica*, L., and *Naravelia zeylanica*, DC. Some of the vessels [1] have a very wide lumen (·12 mm. or more in diameter), and their walls are furnished with large bordered pits. The vessels with narrower lumina, and the tracheides, which are also present, possess a spiral band. The wood-parenchyma is restricted to the neighbourhood of the vessels; the wood-prosenchyma is simply-pitted and sometimes filled with starch. The cortex of *Clematis* usually shows collenchyma-strands below the epidermis, which have been described in detail by Ambronn. In *Clematis afoliata*, Buchanan, which is characterized by reduction of its leaves, the primary cortex in a transverse

[1] Here, as in all the subsequent descriptions of the wood, the term 'vessels' always means the pitted vessels of the secondary wood.

ection of the stem shows a regular alternation of plates of hard bast and of ssimilatory tissue. The plates of hard bast reach from the epidermis to he soft bast and correspond with the phloem-groups of the vascular bundles Diels). In the pericycle a composite and continuous sclerenchymatous ring sually occurs. On the inner side of the latter the first ring of cork arises. entitel-formation is entirely wanting in *Clematis*. The later periderm-ormations are developed parallel to the first ring of cork, so that a ring-ark is produced. During the increase of the phloem, arched groups of econdary hard bast arise in it. According to Marié, the structure of the ortex of *Naravelia* shows no differences from that of *Clematis*. According to lentovich, the pith of *Clematis Vitalba* is heterogeneous. The innermost art of it soon disappears and is replaced by a cavity.

With regard to the stem of the **herbaceous species** it must first of all e pointed out that the species of *Actaea*, *Cimicifuga*, and *Thalictrum* belong to he anomalously constructed Dicotyledons, because, in a transverse section of he stem, the vascular bundles are arranged in several indistinct circles. Sanio as shown that the innermost of these bundles arise first, and J. E. Weiss has hown that they pass out into the leaf at the next node above, while the peri-heral strands represent the continuation of the leaf-traces of the higher inter-odes. The vascular bundles of *Anemone japonica* (according to J. E. Weiss) ave an analogous course ; in this species medullary bundles occur within the eripheral bundle-ring. Medullary bundles are also found in *Hydrastis* and *laucidium* (Pohl).

The stem of the aquatic species of *Ranunculus* belonging to the section *atrachium* is characterized by the fact that its vascular bundles contain no echanical tissue, but possess a schizogenous air-passage on the inner side of he protoxylem-tracheides. In general our knowledge of the stem-structure f the herbaceous species, and of the Ranunculaceae as a whole, is best shown y the synoptical table in Alb. Meyer's treatise, which can only be referred to hortly. In that work the characters chiefly employed for distinguishing the pecies investigated are :—the varied nature of the pericycle (presence or bsence of hard bast ; the occurrence of a ring of stone-cells, to the inner side f which the primary bundles of hard bast are applied ; or the occurrence of composite and continuous ring of sclerenchyma) ; the varied mode of ifferentiation (as a ring or as strands) of the cortical collenchyma and of the oft bast ; the development of a sclerenchymatous medullary sheath ; and he nature of the interfascicular tissue.

NOTE.—For root-structure see Bonnier, Lohrer, Marié, Maxwell and Prantl ; or abnormalities in tubers of *Aconitum* see Hartwich, Bot. Centralbl., 1897, and he older literature quoted there.

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DILLENIACEAE.

1. Review of the Anatomical Features. The following characters must be specially pointed out as applying to the Dilleniaceae: (*a*) with regard to the structure of the axis:—the bordered pitting of the wood-prosenchyma; the frequent occurrence of broad medullary rays in the xylem; the scanty development of wood-parenchyma; the tendency to the formation of scalariform perforations in the vessels, these being present either exclusively or side by side with simple perforations, the latter then predominating; (*b*) with regard to the structure of the leaf:—the lack of a uniform characteristic stomatal apparatus. Glandular hairs are absent; the hairy covering consists of simple unicellular hairs and of stellate hairs (Fig. 2, *A-C*), rarely (*Hibbertia lepidota*, R. Br., Fig. 2, *D-E*) of peltate hairs. Oxalate of lime is deposited exclusively in the form of bundles of raphides. It must also be noted with regard to the structure of the axis, that the formation of cork is mostly internal and that the outer limit of the bast (the pericycle) varies in its nature. Anomalous stem-structure is found in the species of the genus *Doliocarpus*, in which the original ring of vascular bundles becomes surrounded by concentric secondary bundle-rings, which arise in the pericyclic parenchyma. Finally, there remain to be mentioned: the silicification of epidermal cells of the leaf occurring in many members of the Order; the spicular cells filled with a white secretion in the pith of *Davilla, Doliocarpus,* and *Tetracera*; and the occurrence of spicular cells in the leaf of *Hibbertia grossulariaefolia*, Salisb., and *H. linearis*, R. Br.

2. Structure of the Leaf. There are investigations by Vesque, and more recently by Steppuhn, dealing with the leaf-structure. The investigations of the latter author, which also extend to the structure of the axis, refer to comprehensive material, including many species, of the genera *Davilla, Curatella, Doliocarpus, Tetracera, Acrotrema, Schumacheria, Dillenia, Hibbertia,* and *Pachynema.*

With regard to the **epidermis** of the leaf it must be stated, in the first place, that its cells either have straight or undulated lateral walls. The stomata are usually surrounded by an indeterminate number of cells which are not specially differentiated by their shape; in *Tetracera oblongata,* DC., on the other hand, they are accompanied by subsidiary cells placed parallel to the pore. In the first of these cases (according to developmental investigation of *Dillenia speciosa* by Vesque) the mother-cell of the pair of guard-cells is cut off by the first division. The **leaf-structure** is mostly bifacial; centric leaf-structure occurs only in the leaves of *Hibbertia,* which in some cases are flat, in others have an ericoid character, and in the latter case sometimes show furrow-formation on the lower side. Connected with the furrow-formation just mentioned is the occurrence (in one species—*H. rhadinopoda,* F. v. Müll.) of expansive cushions ('Schwellpolster' of Tschirch)[1], which cause a rolling in of the leaf-margins in the well-known manner when there is a scarcity of water, and a re-extension of the leaf when fresh water is supplied. In the mesophyll of two species of *Hibbertia* (*H. grossulariaefolia,* Salisb., and *H. linearis,* R. Br.) Steppuhn has observed the occurrence of thick-walled and branched spicular cells reaching from one epidermis to the other. He points out the following facts with regard to the structure of the **midrib**. It possesses a stem-like structure, namely a closed ring of vascular bundles in *Curatella, Davilla, Doliocarpus,* and *Tetracera.* In *Acrotrema* and *Dillenia* the midrib contains several (2–7, rarely more) concentric bundles with peripheral phloem; in *Schumacheria* several collateral bundles, arranged in a circle, but free. Differences occur with respect to the presence or absence of mechanical tissue accompanying the bundles of the veins, and are of importance only for purposes of more special diagnosis (see Vesque).

As regards **oxalate of lime**, it has already been pointed out under the general diagnosis, that in the parenchymatous tissues of the axis and leaf it is to be found only in the form of bundles of raphides. The latter have been met with in all the species investigated. Those found in the leaf-tissue, according to Baillon, sometimes cause roughnesses of the leaf-surface, which may be felt by the finger. Not every case of roughness of the leaves of the Dilleniaceae, however, is to be referred to this anatomical feature. It is in some cases caused by groups of silicified cells in the epidermis. Silicification of cell-walls and perhaps also deposition of silica in the cell-cavity appears to be a very wide-spread phenomenon in the Order. Groups of silicified cells in the epidermis of the leaf[2] have been demonstrated by Mohl in *Davilla,* by Baillon in *Curatella,* by O. Bachmann in species of *Doliocarpus, Hibbertia, Pinzona,* and *Pleurandra,* and lastly by Kohl in *Delima.* The silicified cells of these plants occur in groups of either few or several cells; in the latter case they not infrequently group themselves like a rosette round one or several sclerenchymatous hairs, and thus by their prominence in the dry leaf form a knob-like structure, or resemble a small peltate scale (false peltate scale in the latter case). In the interior of the leaf-tissue of *Davilla brasiliana,* DC., solid masses of silica are stated by Mohl to fill the entire cell-cavity together with the pit-canals.

At this point we may also mention the spicular cells, which are filled with peculiar whitish contents (probably not silica), and occur in the **pith** of some

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[1] Tschirch, Beitr. z. Anatomie u. dem Einrollungsmechanismus einiger Grasblätter; Jahrb. f. wiss. Bot., Bd. xiii, 1882, p. 544 et seq.

[2] It is uncertain how far these coincide with the spiny hairs to be mentioned later.

Dilleniaceae. They are elongated, sclerosed, but wide-lumened cells, which had already been seen by Crüger in *Doliocarpus Rolandri*, Gmel., and described by him as special vessels ('eigene Gefässe'), and have since been observed by me in *Davilla rugosa*, Poir. (syn.: *D. brasiliana*, DC.), and by H. Schenck in *Tetracera Breyniana*, Schlecht, and *T. oblongata*, DC.[1]

With regard to the **hairy covering**, the lack of glandular hairs must once more be specially pointed out. The clothing hairs that occur are simple unicellular trichomes, stellate hairs, and in one case (*Hibbertia lepidota*, R. Br.) peltate hairs. The simple unicellular trichomes are very short and papilliform or elongated. The stellate hairs (*Curatella*, *Hibbertia*) consist of a tuft of simple hairs, which is usually embedded in a small multicellular elevation resembling

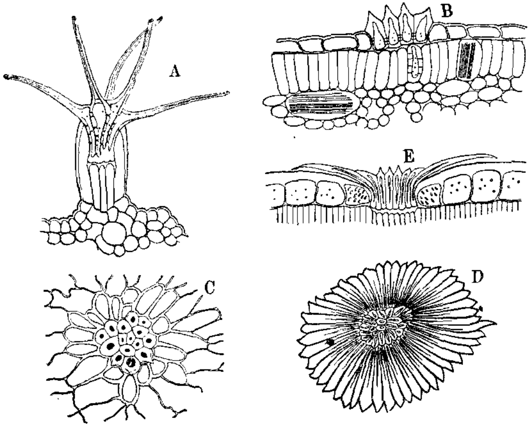

FIG. 2. A, stellate hair of *Hibbertia furfuracea*, Benth. B–C, spiny hair of *Tetracera oblongata*, DC.: B, transverse section through the spiny hair and through a piece of leaf-tissue. C, surface-view of the spiny hair with the surrounding cells of the upper side of the leaf. D–E, peltate hair of *Hibbertia lepidota*, R. Br.: D, in surface-view; E, in section.—Original.

a pedestal (Fig. 2, *A*). The walls of both the simple and the stellate hairs are sometimes incrusted with silica. A special form of stellate hair is presented by the spiny hairs, which are present according to Steppuhn in species of *Tetracera* (Fig. 2, *B–C*) and *Curatella*, and appear to the naked eye as false peltate scales. They consist of a group of epidermal cells, which are produced into short, papilla-like, pointed and strongly silicified hairs. Below this group of cells, single cells of the palisade-tissue are sometimes sclerosed, e.g. in *Tetracera oblongata*, DC., according to my own observation. It is on account of these hairs that the leaves of many of the species concerned are employed in Brazil and in India in the same way as glass-paper for smoothing and cleaning wood,

[1] Gilg and Steppuhn are wrong in denying the presence of contents in the elements in question; the contents are, however, not easy to observe.

metal, &c. The peltate hairs of *Hibbertia lepidota* have already been described, but quite insufficiently, by O. Bachmann and Steppuhn. The shield-like part (Fig. 2, *D–E*) consists at its periphery of a large number of narrow, thick-walled and narrow-lumened ray-cells, which penetrate to a greater or less distance towards the centre of the shield, and then bending downwards join in the formation of the peripheral part of the stalk of the peltate hair. The middle of the shield is occupied by the central sclerenchymatous stalk-cells, which, having reached the surface of the shield, either terminate at once, and in that case end in a small, pointed, siliceous papilla, or are continued for a short distance further in the radial direction and parallel to the surface of the shield, causing a local doubling of the cell-layer of the shield. In correspondence with this the peltate hair may be derived from a group of numerous spiny hairs, if one imagines the peripheral cells of the group elongated into ray-cells and united together to form a shield.

3. STRUCTURE OF THE AXIS. The following description is based on the statements in the works of Baillon, Möller, Solereder, Hitzemann, and Steppuhn, which are cited below.

The peculiar, elongated, thick-walled pith-cells, which are filled with secretion and occur in species of *Davilla, Doliocarpus*, and *Tetracera*, have already been referred to above. With regard to the structure of the pith, one must also mention Baillon's statement as to the occurrence of septation of the pith without sclerosis in most species of *Wormia*, and further, the statements of Hitzemann and Steppuhn as to the occurrence of groups of stone-cells in the pith in species of *Curatella, Davilla, Dillenia, Doliocarpus*, and *Tetracera*, and of solitary stone-cells in species of *Hibbertia*.

In a transverse section through the **wood** the most noticeable feature is that the vessels are scattered. Their diameter varies, and attains a considerable size in the lianes, especially in the climbing species of *Doliocarpus* and *Tetracera*, which in their native country are called 'Water-lianes' (*Bejuco de agua*) in reference to the possibility of obtaining the quantity of water contained in their wide vessels. The vessels of the Dilleniaceae either possess scalariform perforations only, often with a large number of bars, but now and then with a smaller number (species of *Candollea, Dillenia, Hibbertia*), or simple perforations side by side with the scalariform ones (species of *Curatella, Davilla, Doliocarpus, Tetracera*); *in the latter case the scalariform perforations usually only have* a few bars. The wood-prosenchyma forming the groundwork of the xylem has bordered pits throughout, and forms a character of the Order, as had already been pointed out by Baillon for the species investigated by him. The medullary rays vary in breadth. *Candollea, Curatella, Davilla, Dillenia, Doliocarpus, Schumacheria*, and *Tetracera* possess both broad and narrow medullary rays, while *Acrotrema, Hibbertia*, and *Pachynema* have only narrow, 1–2-seriate rays. The medullary rays are throughout of considerable height, and are usually distinguished by containing abundant tannin. The cells of the broad medullary rays are elongated in the vertical direction, but are never very high. The wood-parenchyma is for the most part only slightly developed; Möller mentions tangential bands of xylem-parenchyma only in the case of a wood described as *Curatella americana*, L.

As regards the structure of the **cortex**, in the first place, essential differences occur with respect to the nature of the boundary between the primary and secondary cortex and as to the place of origin of the cork.

According to Hitzemann, a composite and continuous ring of sclerenchyma is present on the outer side of the bast in *Dillenia pentagyna* and *D. speciosa*, as well as in *Tetracera madagascariensis*. This is replaced by a ring of bast-fibres in *Hibbertia grossulariaefolia* and *H. volubilis*, and, according to Steppuhn, in the majority of the Dilleniaceae. The ring just mentioned is also indicated in *Candollea*

cuneiformis by some few bast-fibres. Isolated bundles of bast-fibres are also found in the outer part of the pericycle in species of *Davilla, Doliocarpus,* and *Tetracera* (according to H. Schenck). Finally, no demarcation of the pericycle by sclerenchyma is present in *Tetracera euryandra,* according to Hitzemann, and in *Acrotrema* and some of the species of *Hibbertia,* according to Steppuhn.

Cork-formation is internal in most members of the Order; that is to say, the cork usually arises in the inner layers of the primary cortex (*Doliocarpus,* according to H. Schenck) or at the outermost limit of the soft bast—if a ring of bast-fibres is present, interior to it—e.g. according to Hitzemann in *Candollea, Davilla, Hibbertia,* and *Tetracera.* In *Dillenia,* on the other hand, the cork, according to Hitzemann, originates sub-epidermally in the outermost cell-layer of the primary cortex. The cork-cells vary in structure. They sometimes have large lumina and delicate walls, as in *Dillenia pentagyna,* Roxb. (according to Möller); in other cases some of them are sclerosed on one side, e.g. in *Dillenia speciosa* or *Tetracera madagascariensis,* or sclerotic on all sides, as in *Tetracera euryandra*; in the last-named species the stone-celled cork forms layers which are concentric and alternate with thin-walled cork.

As regards the **secondary cortex,** scattered bast-fibres may occur in it (in species of *Davilla, Doliocarpus,* and *Tetracera,* according to H. Schenck), and also groups of stone-cells (in species of *Curatella, Davilla, Doliocarpus,* and *Tetracera,* according to Steppuhn, and in *Dillenia pentagyna,* according to Möller).

Tannin is found abundantly in the cortex, just as in the medullary rays of the wood.

Anomalous stem-structure is at present known only in the genus *Doliocarpus.* Other climbing shrubs belonging to the genera *Davilla* and *Tetracera,* collected and investigated by H. Schenck, are normal in structure. The anomaly of *Doliocarpus* consists in the formation of successive concentric rings of bundles, which takes place only in rather thick portions of the axis. The secondary rings of bundles always arise outside the outermost phloem-elements of the original bundle-ring, in the parenchymatous pericycle and internally to the primary groups of bast-fibres. It is worth noting, that in the xylem of the secondary bundles no primary forms of tracheae are produced, and that the secondary bundles are separated from one another by fairly broad medullary rays. Crüger was the first to discover the anomaly in question, and mentioned it for *Doliocarpus Rolandri,* Gmel., and for a large undetermined Dilleniaceous species from Trinidad, called *Bejuco de aqua* or Water-liane. The latter, described by H. Schenck as probably identical with *Pinzona calineoides,* Eichl., belongs, according to Steppuhn, to *Doliocarpus scandens* (Aubl.) Gilg.

Literature: Crüger, Bot. Zeit. 1850, p. 166.—Mohl, Bot. Zeit. 1861, p. 209.—Eichler, in Flora brasil., vol. xiii, 1, 1864, p. 116.—Baillon, L'anatomie des D., Adansonia vii, 1866–7, pp. 88–93; see also Compt. rend., t. lxiv, 1867, p. 297, and Baillon, Hist. des plantes, t. i, 1867–9, p. 119 et seq. —Möller, Holzanatomie, Denkschr. Wiener Akad. 1876, pp. 70 and 366.—De Bary, Vergl. Anat., 1877, p. 102.—Vesque, Nouv. Arch. du Mus. d'hist. nat., sér. 2, t. iv, 1881, pp. 29–31 and pl. i.—Möller, Rindenanatomie, 1882, p. 231.—Radlkofer, Abb. des naturw. Ver. zu Bremen, Bd. viii, 1883, p. 439.—Blenk, Durchs. Punkte, Flora 1884, p. 381.—Solereder, Holzstruktur, 1885, p. 47.—O. Bachmann, Schildhaare, Flora 1886, separate copy, pp. 28 and 39.—Hitzemann, Vergl. Anatomie der Ternströmiaceen, etc., Diss., Kiel, 1886, pp. 57–77.—Douliot, Périderme, Ann. sc. nat., sér. 7, t. x, 1889, pp. 341–2.—Kohl, Kalksalze u. Kieselsäure, Marburg, 1889.—H. Schenck, Anatomie de Lianen, 1893, pp. 73–7 and p. 252 and Tab. III, Figs. 24–8.—Gilg, in Natürl. Pflanzenfam., iii. Teil, Abt. 6, 1893, pp. 101–3.—Steppuhn, Vergl. Anat. der D., Diss., Bern, 1895, 30 pp. and 2 Tab. (separate copy from bot. Centralbl. 1895, Bd. lxii).

CALYCANTHACEAE.

1. Review of the Anatomical Features. This small Order is excellently characterized anatomically by the presence in the stem of four cortical vascular bundles inversely orientated as regards the position of their xylem- and phloem-groups (Fig. 3, *C*), and by the possession of secretory cells (Fig. 3, *B*). To these must be added the following important positive and negative characters: simple unicellular sclerosed hairs, which together with their subsidiary cells are silicified (Fig. 3, *A*); the lack of glandular hairs; stomata, which are accompanied by two subsidiary cells parallel to the pore; the absence of a ring of sclerenchyma in the pericycle, instead of which there are isolated groups of primary bast-fibres; the origin of the cork immediately below the epidermis and the radial elongation of the first-formed periderm-cells; narrow medullary rays in the wood; spirally thickened, pitted vessels with

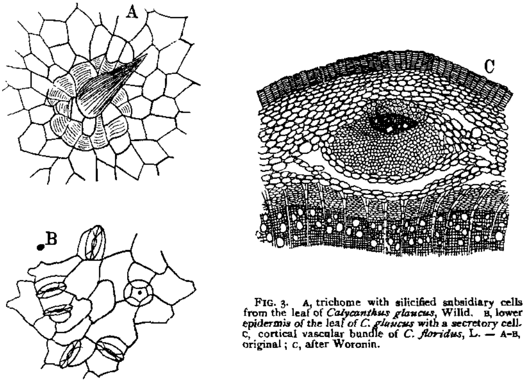

Fig. 3. A, trichome with silicified subsidiary cells from the leaf of *Calycanthus glaucus*, Willd. B, lower epidermis of the leaf of *C. glaucus* with a secretory cell. C, cortical vascular bundle of *C. floridus*, L. — A–B, original; C, after Woronin.

simple perforations; the relatively small production of wood-parenchyma; the pits of the wood-prosenchyma with a small but often evident border. Oxalate of lime is only rarely produced, and then in the form of small prismatic crystals; tannin is absent.

2. Structure of the Leaf[1]. The leaves of the Calycanthaceae are bifacial in structure. The **epidermal cells** have straight or curved lateral walls. Palisade-parenchyma is present, for example, in *Chimonanthus fragrans* and *Calycanthus laevigatus*, but is indistinct in *Calycanthus floridus*. The stomata are found only on the lower side of the leaf, and are always accompanied by two subsidiary cells placed parallel to the pore. Sclerenchyma accompanying the vascular bundles of the veins may be present or absent.

The **hairs** are exclusively unicellular, they may be short or rather long, and are strongly thickened; both they and the neighbouring cells, which surround

[1] Chiefly according to Vesque, Blenk and Lignier, ll. cc.

them in rosette-fashion, possess strongly silicified membranes (Fig. 3, *A*). In dried leaves the groups of silicified cells in question give rise to dots, which may either be dark (*Calycanthus laevigatus*), or, more commonly, dimly translucent. Glandular hairs are absent.

Secretory cells are present in all the members of the Order in the parenchymatous tissues of the axis, leaf and root as well as in those of the reproductive organs. They can be easily recognized by their spherical form and oily contents; according to Höhnel, the wall of these elements in *Calycanthus floridus* exhibits a thin middle-lamella, a very thin suberized and a thicker lignified lamella. In the leaf the secretory cells occur in the mesophyll as well as in the epidermis of the lower side (see Fig. 3, *B*). Each epidermal secretory cell, only a small part of which contributes to the formation of the free surface of the lower epidermis, has a small pit ('petits granules brillants centraux' of Lignier) in the middle of its outer wall.

Further, it deserves notice, that, according to Lignier, tannin is not present in the leaf or in the stem (with the exception of the cork-tissue).

Oxalate of lime is either not present at all, or is only differentiated in the form of small prismatic crystals, which appear to belong to the tetragonal system.

3. STRUCTURE OF THE AXIS. A specially characteristic feature is the occurrence of **four vascular bundles** (Fig. 3, *C*) **in the primary cortex**, discovered by Mirbel in *Calycanthus floridus* and since observed in all members of the Order. In rather stout branches these bundles form raised longitudinal lines. Like the normal ring of bundles they possess secondary growth in thickness, and it is a specially essential feature that they are inversely orientated as regards the position of their xylem- and phloem-groups. The xylem lies on the outer side, the phloem on the inner. These cortical vascular bundles, like those of the normal bundle-ring, are leaf-traces. Each of the opposite, decussate leaves shows three vascular bundles in its petiole, one larger median one, and two smaller lateral ones; at the node the stronger median bundle enters the bundle-ring, while the two lateral ones rotate through 180°, so that their xylem-groups assume the inverted orientation, and they then pass downwards in the cortex parallel to the bundles of the ring, and at the next node insert themselves on the lateral bundles, which enter there [1].

The following facts must be mentioned with regard to the **wood**. The medullary rays are narrow, 1–2-seriate. Some of the vessels have rather large cavities (up to ·06 mm. in diameter), and both they and the tracheides possess a spiral thickening of the wall as well as bordered pits; the walls of the vessels have simple pits where they are in contact with the parenchyma of the medullary rays. The perforations of the vessels are always simple. Wood-parenchyma is only slightly developed. The wood-prosenchyma has slit-like pits with a small, often distinct, border.

The **cortex** contains no ring of sclerenchyma. On the outer side of the bast only isolated groups of bast-fibres are present. The cork in *Calycanthus* and *Chimonanthus* arises in the outermost cell-layer of the primary cortex. The first-formed periderm-cells are radially elongated. In the primary cortex of relatively thick branches small plates of sclerotic cells are found, these cells having only their inner tangential walls sclerosed. The secondary cortex forms neither bast-fibres nor stone-cells; its parenchyma is distinguished by its loose texture.

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[1] The statements of Hérail (loc. cit.), according to which the cortical bundles arise in the pericycle and subsequently move outwards, cannot be brought into agreement with the above, and require confirmation.

The pith is heterogeneous in *Calycanthus floridus*, according to Mentovich. The peripheral cells are very small and thick-walled, and in winter are filled with starch-grains; the cells of the central part are much larger, less thickened and empty; the latter, moreover, have secretory cells among them.

Secretory cells occur in the axis both in the pith, the secondary and primary cortex, and in the epidermis.

Literature: Mirbel, Tige d'un très vieux *Calycanthus floridus*, Ann. sc. nat., sér. 1, t. xiv, 1828, p. 367, pl. xiii.—Gaudichaud, Arch. de bot., t. ii, 1833, p. 493.—Treviranus, Phys. d. Gew., 1835, i. Taf. I.—Lindley, Natural System of bot., 1836, p. 160, and Vegetable Kingdom, 1846, p. 541.—Treviranus, Bot. Zeit. 1847, p. 377.—Henfrey, Annals and Magaz. of Nat. Hist., ser. 2, vol. i, 1848, p. 124.—Lindley, Introduction to bot., i, London, 1848, p. 209.—Crüger, Anomale Holzbild., Bot. Zeit. 1851, p. 481.—Sanio, Kork, Pringsheim Jahrb., Bd. ii, 1860, p. 39 et seq.—Woronin, Bau des Stammes von *Calycanthus*, Bot. Zeit. 1860, p. 177.—Sanio, Kork, Pringsheim Jahrb. 1860.—Möller, Holzanatomie, Denkschr. Wiener Akad. 1876, pp. 72 and 368.—De Bary, Vergl. Anat., 1877, p. 268.—Höhnel, Sekretionsorg., Sitz.-Ber. Wiener Akad., Bd. lxxxiv, Abt. 1, 1881, p. 594.—Vesque, Nouv. Arch. du Mus. d'hist. nat., sér. 2, t. iv, 1881, pp. 31–4 and pl. ii.—Möller, Rindenanatomie, 1882, p. 364.—Blenk, Durchsichtige Punkte, Flora 1884, p. 55 et seq., separate copy, pp. 9, 10.—Lignier, Les massifs libéro-ligneux corticaux etc., Bull. Soc. bot. de France, t. xxxi, 1884, p. 128.—Mentovich, Markgew., Klausenburg, 1885, Hungarian, abstract in Just 1885, i, p. 789.—Solereder, Holzstruktur, 1885, p. 48.—Hérail, Tige des Dicotyled., Ann. sc. nat., sér. 7, t. ii, 1886, p. 236.—Plitt, Anat. d. Blattstiele, Diss., Marburg, 1886, p. 48.—Lignier, Anat. comp. des Calycanthacées etc., Arch. bot. du Nord de la France, Paris, 4° année, n. 38 etc., 1887, pp. 1–150.—Prantl, in Natürl. Pflanzenfam., iii. Teil, Abt. 2, 1888, p. 92.—Solereder, Engler, Bot. Jahrb., Bd. x, 1888, p. 418.—J. E. Weiss, Kork, Denkschr. Regensburger bot. Gesellsch. 1890, p. 67.

MAGNOLIACEAE (EXCL. TROCHODENDREAE[1]).

1. REVIEW OF THE ANATOMICAL FEATURES. The following characters may be pointed out as common to all the Magnoliaceae: the occurrence of secretory cells, the wood-prosenchyma with bordered pits, the tendency to the formation of scalariform perforations in the vessels, as well as the absence of unicellular hairs and of glandular hairs. Further, the type of stoma is characteristic, although not always equally clearly marked: the guard-cells are usually accompanied by two subsidiary cells parallel to the pore. Where hairs are present, they always consist of only one row of cells. There is no ring of sclerenchyma in the cortex; in the pericycle only isolated groups of bast-fibres are present. The origin of the cork is superficial, i.e. in the epidermis, or immediately below it, or at least, in a superficial layer of the primary cortex. Oxalate of lime is present in the form of small octahedral or prismatic crystals, or of clustered crystals, more rarely (Schizandreae) in the form of relatively large individual crystals. For the tribe Magnolieae the occurrence of diaphragms of stone-cells in the pith is characteristic; for *Magnolia*, the presence of branched sclerenchyma-cells in the cortex; for *Illicium*, mucilaginous cells in the palisade-tissue; for the Schizandreae, sclerenchyma-cells, in the walls of which crystals of oxalate of lime appear to be embedded (Fig. 4, *A–B*); for *Drimys* the absence of vessels in the xylem. The following special anatomical features observed in the Order also deserve mention and may be employed for specific diagnosis: papillose differentiation of the lower epidermis of the leaf, mucilaginous cells in the epidermis and in the veins of the leaf, development of a hypoderm on the upper side of the leaf, and so on.

2. STRUCTURE OF THE LEAF. The following statements are based chiefly on the works of Blenk and Vesque, as well as on some original, hitherto unpublished observations.

[1] The Trochodendreae, which Bentham and Hooker included as a tribe of the Magnoliaceae, are here treated as an independent group appended to that Order.

The **epidermal cells** have straight or undulated lateral walls. Their outer walls are sometimes distinctly striated; in other species the cuticle is granulated in consequence of the deposition of wax. Silicification of the epidermis is mentioned by De Bary and Kohl for *Magnolia grandiflora*; in *Magnolia glauca* siliceous masses are found in the interior of the cells (Kohl). The hard epidermis of *Drimys Winteri*, on the other hand, is free from silica. In *Drimys granatensis*, L. f., the cells of the lower epidermis are produced into thick-walled papillae with small lumina; in *Liriodendron tulipifera*, L., and in *Michelia Punduana*, Hook. f. et Th., they are sub-papillose. A hypoderm is developed on the upper side of the leaf in some species, e.g. in *Tasmannia aromatica*, owing to the occurrence of division-walls parallel to the surface of the leaf in the epidermal cells; this is still more pronounced in *Manglietia insignis*, Bl., in the neighbourhood of the large veins, and especially so in *Magnolia grandiflora*, L., *Michelia excelsa*, Bl., *M. Punduana*, Hook. f. et Th., and *Talauma ovata*, St. Hil. The stomata are, as a rule, only found on the lower side; more rarely they occur on the upper side as well, though in smaller numbers, e.g. in *Kadsura japonica*, Juss. Vesque states that in the Magnoliaceae (including Schizandreae), the guard-cells are always accompanied by two lateral subsidiary cells, which are parallel to the pore; here the division takes place in such a way that the formation of the subsidiary cells precedes that of the mother-cell of the guard-cells (Rubiaceous type). According to my own observations, however, this type is obliterated in places in the mature leaf of the Schizandreae, e.g. in *Schizandra nigra*, Maxim., *S. axillaris*, Hook. f. et Th., and *Kadsura japonica*, Juss., all of which have a large oval pair of guard-cells. Lastly, the lobe-like appendages of the two guard-cells of *Illicium Griffithii*, Hook. f. et Th. and *I. religiosum*, Sieb. et Zucc., are also worth mentioning. The appendages lie in the direction of the pore.

The **mesophyll** is usually bifacial in structure, and moreover exhibits a series of differences, which may be utilized for specific diagnosis. The same holds good for the structure of the veins, in which sclerenchyma may or may not be developed.

With regard to the arrangement of the vascular bundles in the **midrib** and in the petiole, one gathers from the investigations on this subject by Vesque, Plitt, and Petit, that the bundles in the Wintereae (*Drimys, Tasmannia, Illicium*) and in the Schizandreae are arranged in the form of an arc, in the Magnolieae (*Magnolia, Talauma, Michelia*, and *Liriodendron*), on the other hand, in a circle, in which case accessory bundles may also be present at the sides of the groove on the upper side of the petiole.

An excellent character for the whole Order is afforded by the spherical or lenticular **secretory cells**, which are present in the parenchymatous tissues of the leaf and axis, are filled with resin or ethereal oil, and are provided with a suberized wall. These secretory cells frequently produce transparent dots in the leaves, and have been demonstrated by Blenk in a large number of species of nearly [1] all the genera of the Order. In the leaf they are found chiefly in the spongy parenchyma, more rarely in the palisade-tissue also, and still more rarely (*Kadsura japonica, Schizandra axillaris, S. nigra*) in the lower epidermis as well. In *Illicium floridanum*, Ellis, the secretory cells belong exclusively to the lower epidermis. In the axis they occur in the pith as well as in the cortex.

The three species of *Illicium* investigated by Blenk (*I. floridanum*, Ellis, *I. Griffithii*, Hook. f. et Th., and *I. religiosum*, Sieb. et Zucc.), in addition to the resin-cells, possess **mucilaginous cells** in the palisade-tissue. Moreover, cells

[1] With the exception of *Zygogynum*; but for this genus also the occurrence of secretory cells is fairly certain, because transparent dots in the leaves are described by Baillon (Adansonia, x, p. 334) for *Z. pomiferum*, Baill.

with mucilaginous membranes occur also in the Schizandreae. Blenk mentions mucilaginous epidermal cells of the leaf in *Schizandra axillaris*, Hook. f. et Th., and *S. elongata*, Hook. f. et Th., and mucilaginous cells in the vascular bundles of the leaf-veins of *S. axillaris*, *S. chinensis*, C. Koch, *S. elongata*, and *S. nigra*, Maxim. Vesque also saw the latter cells, and called them 'lacunes à gomme,' and he met with analogous mucilage-receptacles (' Schleimgänge ' of Prantl) in the bast of the axis of *Sphaerostemma propinquum* and *Kadsura japonica* (see also Parmentier).

Oxalate of lime appears according to Vesque to be absent in the leaf-tissue of the Wintereae. Clustered crystals as well as solitary crystals have been stated by Möller to occur in the cortex of a plant described as *Illicium anisatum*. In the Magnolieae [1] only small clustered crystals or small prismatic or octahedral crystals have been observed by Vesque in the leaf and by Möller in the cortex. Larger solitary crystals of prismatic or octahedral form are found in the Schizandreae only.

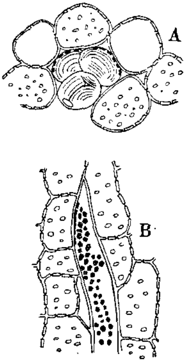

FIG. 4. Crystal-bearing fibrous cells from the pith of *Kadsura Roxburghiana*, Arn.: A, in transverse section; B, in longitudinal section. The crystals are shaded.—Original.

Following on the discussion of the features of the crystals the occurrence of **crystal-sclerenchyma** in the Schizandreae (Fig. 4, *A*–*B*) may be mentioned. This tissue consists of rod-shaped sclerenchyma-cells, which are pointed at the ends and have very thick walls, in which solitary crystals of oxalate of lime appear to be embedded. Closer examination of these spicular cells, several of which sometimes lie together, proves that the crystals are not situated in the wall, but in the remnant of the cell-lumen, which by strong unequal thickening of the wall is shifted towards the periphery of the cell. In those portions of the spicular cells, by which the latter are in mutual contact, excretion of crystals does not take place. The spicular cells in question were first discovered by Vesque in the pith of *Kadsura japonica*; they also occur, according to my own casual observations, in the pith and cortex of *K. Roxburghiana*, Arn., in the cortex of *Schizandra nigra*, Maxim, and in the larger veins of the leaf in *Kadsura japonica*, Juss., and *Schizandra axillaris*, Hook. f. et Th. Spicular cells of another kind, namely branched sclerenchyma-cells, may be described as characteristic of the members of the tribe Magnolieae. They occur in the latter quite generally in the primary cortex, often in the pith and sometimes (e.g. in *Manglietia insignis*, Bl., *Michelia Punduana*, Hook. f. et Th., &c.) also in the ground-parenchyma of the larger veins.

The **hairy covering** consists only of simple uniseriate hairs. Unicellular trichomes as well as glandular hairs are absent. The cells of the uniseriate hairs are either of equal length (*Liriodendron*), or two or three short basal cells are followed by one or several longer hair-cells. The walls of the hair are either uniformly thickened, or more rarely (*Michelia*) thickened on one side, similarly to those of *Clematis*.

3. STRUCTURE OF THE AXIS. The **pith** of the Magnoliaceae is heterogeneous

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[1] The statement in the literature (Kohl, loc. cit., p. 35) that crystal-sand occurs in *Liriodendron* is incorrect; with regard to this see also Arcangeli, *Nuovo Giorn. bot.*, vol. xxiii, 1891, p. 367 et seq.

according to Gris. Usually it consists, towards the centre, of empty cells with rather large cavities, and, at the periphery, of thick-walled active cells. A more or less distinct septation of the pith by diaphragm-like groups of sclerosed cells, some of which are still active, is characteristic of the Magnolieae

The **xylem** (for more detail on this see Groppler, loc. cit.) is primarily characterized by wood-prosenchyma with bordered pits. The medullary rays are either fairly broad (attaining a breadth of 5 cells in *Talauma*, 7 in *Manglietia*, and 10 in *Drimys*), or narrow (2–4 cells broad in the remaining genera), and are always distinguished by their considerable height in the vertical direction. The cavities of the vessels are of various sizes. The perforations of the vessels in some of the species are exclusively scalariform, and in that case they usually have very numerous bars (now and then more than 100); in other species scalariform perforations with few bars are present, side by side with which simple perforations may sometimes (species of *Magnolia, Kadsura, Schizandra*) occur. Where the walls of the vessels are in contact with one another, scalariform bordered pits are frequently found in the Magnolieae; where in contact with medullary-ray-parenchyma, the wall of the vessel bears large, simple, elliptical, but also small, simple pits, the latter graduating in places into bordered pits. Spiral thickening of the walls of the vessels has been observed in *Magnolia grandiflora, Michelia Cathcartii*, Hook. f. et Th., *M. Punduana*, Hook. f. et Th., and *Talauma Rumphii*, Bl. In most members of the Order wood-parenchyma is rather abundantly developed in the autumn-wood, in *Drimys* it is very scanty; in *Michelia longifolia* it forms rather broad transverse bands.

As compared with the other Magnoliaceae[1], the genus *Drimys* (including *Tasmannia*) forms an extremely noteworthy exception as regards the structure of the wood, vessels being completely absent in this genus, as Goeppert was the first to observe. The structure of the xylem of *Drimys* consequently recalls the wood of the Coniferae and especially that of the Araucarieae. Apart from the spiral and scalariform tracheae of the primary wood, in which also true perforations are absent, the whole of the xylem consists of wood-prosenchyma, the elements of which have bordered pits and are square in cross-section, and of narrow or rather broad medullary rays with their cells elongated in the vertical direction. The bordered pits of the prosenchyma of *Drimys* have large circular borders and crossed slit-shaped openings to the pit-cavities.

The following table is the best method of shortly summarizing the varying features in the special **structure of the wood**, together with some characteristic features in the pith, in the tribes and genera of the Magnoliaceae:

I. Perforations of the vessels scalariform, with very numerous bars, or no perforations in consequence of absence of vessels: Wintereae.

(1) Vessels absent: *Drimys*.

(2) Vessels present: *Illicium*.

II. Scalariform perforations, with not very numerous bars (usually 1–15, rarely up to 25), and sometimes also simple perforations: Magnolieae and Schizandreae.

(1) Vessels with relatively small lumen (maximum-diameter = ·045 mm.); wood-prosenchyma, except in *Talauma*, fairly wide-lumened and not thick-walled; groups of stone-cells, more or less like diaphragms, in the pith; no crystal-containing spicular cells: Magnolieae.

(*a*) Very abundant production of vessels; practically the whole of the spring-wood consists of vessels: *Magnolia, Manglietia, Liriodendron*.

(*b*) Vessels less abundant: *Talauma, Michelia*.

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[1] The statement in Roth's abstract of Parmentier's work (Bot. Centralbl. 1895, p. 497), and the subsequent statement of Harms (in Sitz.-Ber. deutsch. bot. Gesellsch. 1897, p. 358), that according to Parmentier *Zygogynum* shares with *Drimys* the lack of vessels, is incorrect. Parmentier has expressly pointed out (loc. cit., p. 623, note) that he had no *Zygogynum* for investigation.

(2) Vessels with fairly large lumen (maximum-diameter = ·09–·11 mm.); wood-prosenchyma rather thick-walled, but not narrow-lumened; crystal-containing spicular cells present, viz. in both pith and cortex or in cortex only: Schizandreae.

Our knowledge of the **cortical structure** of the Magnoliaceae is practically limited to the statements of Möller, who investigated species of the genera *Magnolia, Liriodendron,* and *Illicium*. The formation of cork is superficial. In *Liriodendron* and *Magnolia* the cork arises in the outermost cell-layer of the primary cortex; further, according to Douliot, it is the epidermis itself that becomes the phellogen in *Drimys glauca*, whereas it is the second or third cell-layer below the epidermis in *Kadsura japonica*. In *Magnolia* the **primary cortex** contains groups of stone-cells and branched sclerenchymatous cells, while in *Liriodendron* sclerenchyma is absent. Isolated groups of bast-fibres are found in the pericycle in *Magnolia* and *Liriodendron*. In both these genera the secondary bast is more or less distinctly stratified owing to tangential groups of bast-fibres. The medullary rays of the bast are 3–5-seriate and broadened towards the primary cortex. Lastly, according to Strasburger, it is also worthy of note that the genus *Drimys*, which agrees with the Coniferae in the structure of its wood, resembles a Dicotyledon in the occurrence of companion-cells to the sieve-tubes.

The occurrence of spicular cells, of crystalline excretions, and of secretory cells in the tissues of the axis has already been discussed in describing the leaf-structure.

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TROCHODENDRACEAE[1].

I. Review of the Anatomical Features[2]. The anatomical features common to the five genera are the following: Wood-prosenchyma with bordered pits; stomata, surrounded by several neighbouring cells, which are not of special form; absence of glandular hairs. In other respects numerous differences are

[1] Under this name, as here also, the following five genera have come to be grouped in the course of time: *Trochodendron, Euptelea, Cercidiphyllum, Eucommia* and *Tetracentron*. Of these, however, *Tetracentron* approaches very nearly to the Magnoliaceae, as Harms has rightly pointed out, and, further, *Cercidiphyllum* will without doubt subsequently have to be separated from the Trochodendraceae and probably transferred to the Hamamelideae. (The so-called female flower of *Cercidiphyllum* is an inflorescence; the ventral sutures of the carpels are directed outwards!)

[2] Most important literature: Harms, *Tetracentron* u. d. Fam. d. Trochodendr., in Ber. deutsch. bot. Gesellsch. 1897, pp. 350–60, and in Natürl. Pflanzenfam., Nachtr. and Reg., Teil ii–iv, 1897, p. 158; see also Parmentier in Assoc. franç., Caen, 1894, 2° partie, p. 624, and Ann. Sc. Nat., sér. 8, t. ii, 1896, p. 35.

found. Xylem-vessels are absent in *Trochodendron* and *Tetracentron*; in *Euptelea* and *Cercidiphyllum* the vessels have scalariform perforations with exceptionally numerous bars; in *Eucommia* there are few bars and simple perforations also occur. In the pericycle one finds either a composite and continuous sclerenchymatous ring (*Euptelea, Trochodendron*, and *Tetracentron*) or a loose ring of bast-fibres (*Eucommia*) or only isolated bundles of hard bast (*Cercidiphyllum*). The formation of cork is superficial, as far as is known. Oxalate of lime is present in the form of solitary or clustered crystals, or is absent. Internal secretory organs have been observed only in *Tetracentron* (resin-cells) and *Eucommia* (characteristic caoutchouc-cells). Simple, unicellular trichomes have been met with only in *Eucommia*. Lastly, the occurrence of branched sclerenchymatous cells in the leaf and axis of *Trochodendron* and of siliceous bodies in *Eucommia* must also be mentioned.

2. STRUCTURE OF THE LEAF. The leaves of all the five genera are bifacial in structure. In *Trochodendron* and *Tetracentron* the spongy tissue is distinguished by the presence of large intercellular spaces; in *Trochodendron* the slender arms of the branched sclerenchyma-cells [1], which are differentiated as internal hairs, project into these spaces. It may be added here, that large intercellular spaces and the branched sclerenchymatous cells just described are also present in the axis of *Trochodendron*, namely in the inner part of the primary cortex. Stomata are found only on the lower side of the leaf, and are surrounded by several ordinary epidermal cells. The pair of guard-cells is characterized by its circular outline in *Trochodendron*, and by its large size in *Eucommia*. In *Cercidiphyllum japonicum*, Sieb. et Zucc., and in *Tetracentron* the epidermal cells of the lower side are sub-papillose.

Oxalate of lime has been observed in the form of clustered crystals in the mesophyll of *Cercidiphyllum* and in the cortex of *Euptelea*, in the form of ordinary solitary crystals in the cortex of *Cercidiphyllum, Tetracentron*, and *Trochodendron*. In *Eucommia* oxalate of lime is absent in leaf and axis. In place of it we find in this genus: (*a*) in the leaf, groups of silicified cells, in the formation of which a complex of epidermal cells and palisade-cells lying below them is concerned, in a manner similar to what is found in many Aristolochieae; (*b*) in the axis (in the neighbourhood of the pericycle) stone-cells, which are moderately elongated in the vertical direction, and in some cases have siliceous contents; and, besides these, thin-walled parenchymatous cells (a kind of stegmata), each with one superficially areolate silica-body, these cells being often in pairs.

The **secretory cells** of *Tetracentron* are filled with a resinous secretion and occur in the spongy tissue of the leaf as large branched cells, in the bast and primary cortex of the axis as cells which have fairly wide lumina and are elongated in the direction of the axis. The **caoutchouc-cells** of *Eucommia ulmoides*, Oliv., require a more detailed description. Their occurrence had already been noted by Oliver, and they were more closely investigated by F. E. Weiss [2]. They occur abundantly in the branches and in the leaf, and may be recognized, on merely breaking these organs, as colourless, extensible, elastic threads, in just the same way as in certain species of *Hippocratea*, in the species of the Celastrinean genus *Wimmeria* or of the Apocynaceous genus *Parameria*.

In the branch the caoutchouc-cells occur in the pith, in the bast, and in the primary cortex; in the leaf they accompany the vascular bundles of the veins. They are long cells, which in appearance possess great similarity to the well-known

[1] Compare Blenk, Flora, 1884, p. 52 et seq., Reprint, p. 7 et seq.

[2] The caoutchouc-containing cells, &c., Transact. of the Linn. Soc., ser. 2, vol. iii, Bot., 1892, pp. 243–54, pl. 57, 58.

non-articulated laticiferous tubes. They are, however, essentially different from the latter, as their development shows. While, as is well known, the whole system of non-articulated laticiferous tubes of a plant is in general derived from two or three initial cells in the embryo, the caoutchouc-cells in question, according to Weiss, do not originate in the embryo, but arise subsequently in all the secondarily produced tissues—both in the secondary bast and in the newly produced branches and leaves. At first short, they afterwards grow to a considerable length. Unlike the non-articulated laticiferous tubes, they do not branch, or only here and there form short protuberances, which become somewhat swollen. The ends of the caoutchouc-sacs sometimes also show similar swellings. As to the contents, in the earlier stages of development numerous large caoutchouc-bodies are found in the protoplasm, and subsequently fuse into a homogeneous mass of caoutchouc. Another essential feature is that the caoutchouc-cells contain only one nucleus, never several nuclei, like some of the non-articulated laticiferous tubes.

Lastly, mention must also be made of the capitate, multicellular, **glandular emergences**, which are seated on the crenations of the margin of the leaf in *Cercidiphyllum*, and contain a gummy secretion.

3. Structure of the Axis. With regard to the structure of the **wood**[1] it has already been pointed out above, that the prosenchymatous groundwork has bordered pits in all the members of the Order. The medullary rays in *Euptelea*, *Trochodendron*, and *Tetracentron* may be four cells thick, elsewhere they are 1–2-seriate. Vessels are present only in *Cercidiphyllum*, *Euptelea*, and *Eucommia*; they are absent in *Trochodendron* and *Tetracentron*. The vessels of *Cercidiphyllum* and *Euptelea* do not have a wide lumen (diameter = ·021 mm. and ·036 mm. respectively); they have scalariform perforations with very numerous bars, and are provided with simple pits where they are in contact with the parenchyma of medullary rays. The vessels of *Eucommia* are strengthened by a fibrous spiral band, and possess scalariform perforations only in the neighbourhood of the primary wood; elsewhere they have simple perforations; they bear bordered pits where they are in contact with ray-parenchyma. The wood-parenchyma is scantily developed in the Order.

Trochodendron[2] has a similar xylem-structure to that of the Magnoliaceous genus *Drimys*. Apart from the primary spiral tracheae the wood consists of fibres with bordered pits, and of medullary rays 1–4 cells broad. In transverse section the distinction between spring- and autumn-wood shows up clearly. In transverse section the prosenchymatous cells are quadrangular and are arranged both in radial and in concentric series. In the spring-wood they have large cavities; in the autumn-wood they have thicker walls and are compressed in the radial direction. The prosenchyma-cells of the spring-wood bear scalariform bordered pits on their radial walls, those of the autumn-wood bear bordered pits with circular borders in varying numbers.

The appearance of the xylem-mass of *Tetracentron* in transverse section is the same as in *Trochodendron*, except for the difference that the cells of the wood-prosenchyma are throughout of larger contour. The prosenchyma-cells of the spring-wood have scalariform bordered pits, where their radial walls are in contact, and especially at their overlapping ends. At the places last mentioned the internal openings of the scalariform bordered pits are sometimes slightly wider, and such a series of bordered pits then recalls a scalariform perforation with very numerous bars and very narrow perforation-areas; actual perforation, however, appears not to occur, although a transitional stage to the corresponding structures of *Euptelea* is suggested. Where the prosenchyma of the spring-wood touches the medullary rays, one finds small elliptical (not scalariform) bordered pits. The prosenchyma of the autumn-wood bears bordered pits with more circular borders and in varying number. Besides the

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[1] Solereder, Holzstruktur, 1885, p. 53, and Groppler, Vergl. Anat. d. Holz. d. Magnoliac., Bibliotheca bot. 1894.

[2] Eichler, Flora, 1864, p. 449, and 1865, p. 12; Parmentier's statement (loc. cit.) that vessels occur in *Trochodendron* is incorrect.

medullary rays and the prosenchyma, wood-parenchyma also contributes in a subordinate degree to the composition of the wood. The cells of the parenchyma are strongly elongated in the direction of the axis.

The following points remain to be mentioned with regard to the structure of the **cortex**. The place of origin of the cork is sub-epidermal in *Cercidiphyllum*, epidermal in *Eucommia*. The cork-cells have rather thick walls in *Cercidiphyllum* and *Trochodendron*, thin walls in *Euptelea* and *Tetracentron*, while in *Eucommia* some of them are thickened on one side. The varied nature of the **pericycle** has already been described above in the general diagnosis. Stratification of the secondary bast or occurrence of secondary hard bast, as the case may be, has been observed in *Cercidiphyllum* only.

LACTORIDACEAE.

This small Order, most nearly related to the Magnoliaceae, consists of the monotypic genus *Lactoris*. This genus was erroneously placed with the Piperaceae by Bentham and Hooker; Engler[1] separated it from that Order on grounds of external and anatomical characters and raised it to an independent Order, the Lactoridaceae. Engler makes the following statements with regard to the anatomy of the Order.

Here, as in the Magnoliaceae, secretory cells are found in the spongy tissue of the leaf and in the ground-tissue of the stem. The secretory cells of the leaf give rise to transparent dots. The cells of the lower epidermis of the leaf possess short, rounded papillae. The branches show a xylem-cylinder, which is thick in proportion to the transverse section, and is traversed by medullary rays 2–3 cells broad. The wood contains vessels with bordered pits and simple perforations and wood-prosenchyma bearing bordered pits. There are semilunar groups of primary hard bast in the pericycle, corresponding with the separate vascular bundles. In the pith numerous tannin-sacs occur, which frequently form straight continuous rows.

ANONACEAE.

1. Review of the Anatomical Features. For the recognition of a member of this Order the following characters are of the greatest value: the constant occurrence of secretory cells in the leaf-parenchyma; the almost universal occurrence of solitary or clustered crystals in the epidermis of the leaf (Fig. 6); the stomatal apparatus with its subsidiary cells arranged parallel to the pore; the simple perforations of the vessels; the stratification of the wood due to tangential bands of wood-parenchyma; the frequent occurrence of diaphragms composed of stone-cells in the pith (see Fig. 5) (exception, *Eupomatia*); the stratification of the bast into hard and soft bast (exception, *Eupomatia*); the absence of external glands. In completion of the diagnosis the following may be added. The hairy covering consists of simple, uniseriate, few-celled trichomes, of stellate hairs (*Duguetia, Uvaria*) and of small peltate scales (*Anona, Duguetia*, Fig. 6, *B*). The slit-like pits of the wood-prosenchyma are provided with small, often indistinct, borders (exception: *Eupomatia* with typical bordered pits); the walls of the vessels bear bordered pits where they are in contact with the parenchyma of the medullary rays. The following

[1] Ueber die Fam. d. L., Engler, Bot. Jahrb., Bd. viii, 1887, pp. 53–6; see also Natürl. Pflanzenfam., iii. Teil, Abt. 2, 1888, p. 19, and Solereder, in Engler, Bot. Jahrb., Bd. x, 1889, p. 511.

ıres are found in the leaf-tissue of certain species: mucilaginous cells ›ma, *Habzelia, Rollinia*); sclerenchyma-cells traversing the leaf perpen- larly (*Anona, Duguetia, Guatteria, Habzelia, Unona*), or sclerenchyma-fibres an irregular course (*Anona, Anaxagorea, Guatteria, Popowia, Unona*). The ›tful statement as to anomalous structure of the axis in a species of *Melo- m* (viz. furrowed xylem-mass owing to the presence of four wedges of bast ıing a cross) still requires confirmation.

2. Structure of the Leaf. The general preliminary investigation of the structure by Vesque only extended to a few genera (*Anona, Artabotrys, ıina, Eupomatia, Unona*, and *Xylopia*). From it the following facts may ıthered. The leaf-structure is bifacial, but shows differences, which may be loyed for specific diagnosis; in *Eupomatia Bennettii* the mesophyll exhibits lifferentiation into palisade and spongy e. In the same way the **epidermal cells** their straight or wavy lateral walls afford acters for distinguishing the species; in ıin species of *Artabotrys, Xylopia*, and ıa, the lateral walls of the epidermal cells ar undulated at a high focus, straight at a ocus. The epidermis of the upper side of the in *Anona squamosa* is formed by high cells ;ated like palisade-tissue (Johow). The ata in the species investigated are found on the lower side; they are accompanied, rding to Vesque and Borodin, by subsidiary which are parallel to the pore; the same ies to the genera *Ephedranthus* and *Stormia*, ıtly described by Spencer Moore.

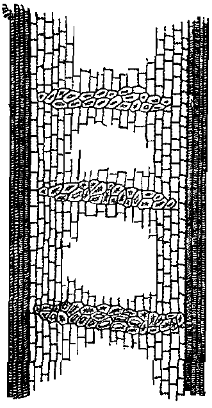

Fig. 5. Septation of the pith by plates of stone-cells in a branch of *Uvaria scabrida*, Oliv.—Original.

The small **veins** are mostly embedded in nesophyll; in *Ephedranthus*, however, ac- ing to Spencer Moore, they are vertically current; their system of vascular bundles companied by bast-fibres. The bundle- m of the secondary veins in large leaves is unded by a sheath of bast-fibres. In the ib an arc of vascular bundles is found in Order. The upper opening of this arc is d by a band of bast-fibres; here also the ılar bundles are accompanied on their lower by abundant hard bast. The structure of ıidrib in *Cananga odorata*, which Guillard has described, is noteworthy; in nsverse section through the midrib of this plant two arc-shaped series of ılar bundles are found.

In all the members of the Order[1] examined, according to the comprehen- investigations of Blenk, **secretory cells** with resinous contents occur in eaf-tissue just as in the Magnoliaceae. They are of spherical or lenticular , and are mostly present in the spongy tissue, more rarely in the palisade- e, and in a series of species (especially species of *Guatteria*) also at the limit lisade and spongy parenchyma. They frequently give rise to transparent

[1] Namely the genera: *Sageraea, Uvaria, Guatteria, Duguetia, Artabotrys, Cananga, Unona, thia, Anaxagorea, Popowia, Goniothalamus, Mitrephora, Rollinia, Anona, Melodorum, ia, Habzelia, Miliusa, Saccopetalum, Orophea, Alphonsea* and *Bocagea*; besides these probably e genera *Ephedranthus* and *Stormia* recently established by Spencer Moore. In these latter retory cells are only described as 'glands' and are figured as resembling secretory cavities than secretory cells.

dots in the leaf. The secretory cells sometimes occur also in the pith and in the primary cortex of the axis. In *Hornschuchia*, which is of doubtful systematic position, the presence of secretory cells suggests, as do other facts, that this genus belongs to the Anonaceae.

In certain species of the genera *Anona*, *Rollinia*, and *Habzelia*[1], cells with strongly mucilaginous membranes are found in the palisade and spongy tissue in addition to the secretory cells; in the latter tissue they are of spherical form. These cells, like the secretory cells, sometimes give rise to transparent dots. In this Order a third kind of minute transparent dot is produced by the occurrence of special spicular cells, i.e. sclerenchyma-cells, which are slightly branched or unbranched, pass perpendicularly through the palisade-tissue, and frequently even traverse the entire thickness of the leaf in this direction; certain species of *Guatteria*, *Duguetia*, *Unona*, *Anona*, and *Habzelia*[2] are characterized by spicular cells of this kind.

Another character distinguishing certain species is afforded by elongated sclerenchyma-fibres in the mesophyll, which mostly run parallel to the surface of the leaf, and are often densely interwoven with one another; they are known

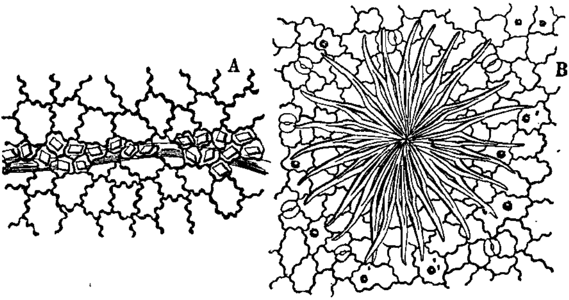

FIG. 6. A, epidermal crystal-cells of *Mitrephora obtusa*, Hook. f. et Thoms. B, peltate hair, with a piece of the epidermis from the lower side of the leaf of *Duguetia bracteosa*, Mart.—Original.

to occur in many species of *Guatteria*, some species of *Anona*, and one species each of *Unona*, *Anaxagorea*, and *Popowia*[3].

Concerning the features presented by the crystals in the leaves of the Anonaceae (Fig. 6), we are quite recently indebted to Borodin for a careful study of the subject. Borodin has made use of the Anonaceae and also of the Violariaceae, in order to show that the study of the crystals may be of very

[1] *Anona acutiflora*, Mart., *A. cinerea*, Dun., *A. cornifolia*, St. Hil., *A. crassifolia*, Mart., *A. micrantha*, Bert., *A. reticulata*, L., *A. sericea*, Dun., *A. spinescens*, Mart., *A. squamosa*, L.; *Rollinia cuspidata*, Mart., *R. laurifolia*, Schlecht., *R. longifolia*, St. Hil., *R. multiflora*, Splitg., *R. orthopetala*, A. DC., *R. resinosa*, Spruce, *R. Sieberi*, A. DC.; *Habzelia obtusifolia*, A. DC.

[2] *Guatteria blepharophylla*, Mart., *G. veneficiorum*, Mart., *Duguetia leptocarpa*, Benth. (in schedula), *D. uniflora*, Mart., '*Unona concinna* or *Helferi*,' Hook. Catalog. (Helfer n. 450); *Anona sessiliflora*, Benth.; *Habzelia obtusifolia*, A. DC.

[3] *Guatteria caniflora*, Mart., *G. cauliflora*, Mart., *G. inundata*, Mart., *G. odontopetala*, Mart., *G. oligocarpa*, Mart., *G. Ouregou*, Dun., *G. Poeppigiana*, Mart., *G. pteropus*, Benth., *G. Schomburgkiana*, Mart., *G. Sellowiana*, Schlecht., *G. subsessilis*, Mart., *G. villosissima*, St. Hil.; *Unona Dasymaschala*, Bl.; *Anona coriacea*, Mart., *A. densicoma*, Mart., *A. foetida*, Mart., *A. monticola*, Mart.; *Anaxagorea brevipes*, Benth.; *Popowia ramosissima*, Hook. f. et Th.

valuable assistance in anatomical classification. On this account I shall deal with these features in somewhat greater detail here. Below I shortly summarize the result of his investigations with regard to the Order, as far as this is possible from the abstract by Rothert in the 'Botanisches Centralblatt.'

The crystalline elements occur in three places: firstly, in the mesophyll; secondly, along the veins, surrounding the vascular bundles of the latter like a sheath; and thirdly, in the epidermis. The first mode of occurrence is inconstant, and is therefore not further considered by the author; the second is very rare. The third is very important and appears in 92 per cent. of the species investigated, so that the presence of crystalline elements (clustered or solitary crystals) in the epidermis must be taken as an ordinal character.

In relation to the form and distribution of the crystals the following six types may be distinguished:

Type I (main type). The epidermal cells contain one clustered crystal each, sometimes also isolated tetragonal octahedra. Borodin has found this type in its pure form in 182 species belonging to 25 genera (52 per cent. of all species investigated). Examples: *Artabotrys*; *Bocagea*; *Rollinia*; most of the species of *Anona* (in nine species crystalline elements are absent in the epidermis); most of the species of *Goniothalamus* (in one species crystalline elements are absent from the epidermis); *Duguetia* and *Asimina* (except one species of each, which belongs to the second type); species of *Melodorum* (compare this genus under type II below). Here also belongs the genus *Stormia*, according to Spencer Moore. *Guatteria*, *Xylopia* and *Popowia* vary between types I and III.

Type II (main type). The epidermal cells contain one oblique (=clinorhombic) solitary crystal each, of varying form and size. This type was observed in its pure form in 56 species belonging to 10 genera. Examples: *Miliusa*; *Orophea* pro parte (the remaining species with transitions to other types; in four species of *Orophea* the upper epidermis of the leaf belongs to the first type, the lower epidermis to the second type); *Melodorum* (with the exception of three species, which come under the first type); one species of *Duguetia* and of *Asimina* (compare these genera under type I).

Type III (derived type). Some but not all of the epidermal cells contain one clustered crystal each, or isolated tetragonal octahedra; the epidermal cells lying between the irregularly arranged crystal-bearing cells possess brown contents. This type is present only in a few species; as also is

Type IV (derived type). Some but not all of the epidermal cells contain oblique (=clinorhombic) solitary crystals, and between them there are irregularly distributed epidermal cells with brown contents as in type III. Example: *Sageraea*.

Type V (derived type). Crystals are found in the epidermis only above the veins and moreover in special cells of smaller size, which also differ from the remaining cells in the thickening[1] of their membranes. Examples: *Mitrephora*, *Alphonsea*; here also belongs *Ephedranthus*, according to Spencer Moore.

Type VI (derived type). The vascular bundles are surrounded by a sheath of crystals; to this type belong only *Stelechocarpus Burakol*, in which species oblique (=clinorhombic) crystals are present in the epidermal cells as well, and *Cyathocalyx zeylanicus*.

It is evident from the examples cited, and may once more be pointed out, that transitions sometimes occur between the types instituted. Further, the distribution of the crystalline elements within the extensive genera *Polyalthia*, *Unona*, and *Uvaria* (at least as these genera are at present limited) presents a quite incongruous appearance, as Borodin allows. But in order to avoid too great hesitation in the employment of the types set up by Borodin for characterizing the genera of this Order, it must on the other hand be pointed out, firstly, that the delimitation of the genera is in many cases not yet firmly established, and secondly, that the above-mentioned transitions occur especially between the two main types on the one hand and the subsidiary types derived from them on the

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[1] I have found that in *Mitrephora obtusa*, Bl. the inner walls of the epidermal cells, i.e. those directed towards the vein, are thickened, and the crystals are inserted on these thickenings.

other; a combination of the two main types themselves is a rare phenomenon, and these main types should therefore primarily be made use of for the diagnosis of the genera.

The **hairy covering** of the Anonaceae consists in part of simple hairs; these are formed by a row of cells of fairly uniform length. In *Unona odorata* and *Xylopia macrantha* the trichomes, according to Vesque, are 3–4-celled; in *Asimina triloba* and *Anona muricata* they are only 2-celled: in these two species the lower cell of the hair is colourless, while the upper one is filled with brown contents. Stellate hairs with unicellular rays occur, according to Blenk, in species of *Duguetia*, and are also mentioned by Bentham and Hooker in the generic diagnosis of *Uvaria*. Peltate hairs (Fig. 6, *B*) are found, according to O. Bachmann, in *Duguetia bracteosa*, Mart., and in *D. Spixiana*, Mart., as well as in *Anona furfuracea*, St. Hil.; these hairs are sunk in the leaf-surface; their very numerous ray-cells are excessively thick-walled, are united to one another for a varying distance, and are more or less distinctly arranged in relation to a median line. Glandular hairs are absent.

3. Structure of the Axis. The structure of the axis also presents a series of good characters distinguishing the Order. It is desirable that the investigations hitherto made on the structure of the axis should be extended by the examination of more abundant material.

Baillon has already drawn attention to the septation of the **pith** of *Anona*, *Artabotrys*, and *Xylopia*, by diaphragms of stone-cells (Fig. 5); these are also found, according to my own investigations, in species of *Unona*, *Uvaria*, *Miliusa*, and *Mitrephora*. It is noteworthy, that in the genus *Eupomatia*, which also deviates considerably from the rest of the Anonaceae, in respect to its external morphological features, groups of stone-cells are wanting in the pith, according to Baillon. In the genera investigated by Molisch, Möller, and by me (viz. *Unona*, *Anona*, *Xylopia*, *Uvaria*, *Miliusa*, and *Mitrephora*), the transverse section of the **xylem**-mass acquires a characteristic appearance, owing to the fact that the woody tissue is traversed by tangential bands of wood-parenchyma, which vary in thickness. The latter are recognizable even with a lens as transverse lines; these are mentioned by Gamble in *Polyalthia* and *Saccopetalum* as well as in *Anona* and *Miliusa*. The medullary rays are 3–6 cells broad. The vessels have a lumen of varying size, and in certain genera, e.g. *Xylopia* and *Cananga*, have a very large cavity (up to ·15 mm. in diameter); the perforations of the vessels are simple, and circular or elliptical. Where the vessels touch one another, bordered pits varying from ·003 to ·006 mm. in diameter occur; bordered pits are found also on the walls of the vessels where they are in contact with the parenchyma of medullary rays. Molisch has discovered crystalline deposits of carbonate of lime in the vessels of *Anona laevigata*, Mart., both in the heart-wood and in the sap-wood of the stem. The wood-prosenchyma usually has fairly thick walls and the lumina are not very narrow[1]; its walls exhibit slit-like pits with small, often indistinct borders. Typical bordered pits in the wood-prosenchyma occur only in *Eupomatia* (Baillon).

Very little is known regarding the structure of the **cortex** in this Order. The origin of the cork has been investigated in *Stormia* only, where it is superficial according to Spencer Moore. According to Baillon, an anatomical character of quite general distribution is the stratification of the secondary cortex into hard and soft bast, similar to what is found in the cortex of the Lime; according to Spencer Moore the same feature is also present in *Ephedranthus* and *Stormia*[2].

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[1] The wood of the Anonaceae is described as 'soft' by Gamble.

[2] It must be remarked here, that in the root of *Anona* the occurrence of primary hard bast (which elsewhere is very rare in the root) has been observed (see Russow, Beitr. über das Leitbündelgewebe, Dorpat, 1875, p. 58).

On the other hand, an exception is in this respect again afforded by the genus *Eupomatia*, which also deviates in other anatomical features (see above). In this genus crescent-shaped groups of hard bast are present only at the outer limit of the phloem, hard bast being absent from the secondary phloem.

In conclusion it remains to be mentioned, that **anomalous stem-structure** has not yet been observed with certainty in the Order, although the latter comprises a series of lianes. The piece of stem of *Melodorum bancanum* (2·5 cm. thick) examined by H. Schenck is normal in structure. On the other hand, an axis with anomalous structure is described by Baillon for a species of *Melodorum* on the authority of a citation of Griffiths (Notul. iv. 707, t. 650, where it is named *Cyathostemma*). From the detailed description of this specimen it seems that this is a case of a xylem-mass furrowed in consequence of four wedges of bast placed like a cross; the wedges of bast show the stratification into hard and soft bast characteristic of the phloem of the Anonaceae.

Literature: Baillon, in Hist. des pl., t. i, 1867–9, pp. 264–8.—Baillon, Adansonia, t. ix, 1868–70, pp. 22–8.—Guillard, Adansonia, t. ix, pp. 107–9.—Möller, Holzanatomie, Denkschr. Wiener Akad. 1876, pp. 70 and 366.—Molisch, Vergl. Anat. des Holzes d. Ebenaceen etc., Sitz.-Ber. Wiener Akad., Bd. lxxx, Abt. 1, 1879, p. 78 et seq. (see also Bd. lxxxiv, Abt. 1, 1881, p. 7 et seq.).—Gamble, Indian Timbers, Calcutta, 1881, pp. 7–10.—Vesque, Nouv. Arch. du Mus. d'hist. nat., sér. 2, t. iv, 1881, pp. 41–4 and pl. 2.—Möller, Rindenanatomie, 1882, pp. 225, 226.—Johow, Pringsheim Jahrb. 1884, p. 308.—Blenk, Flora 1884, p. 56 et seq., separate copy, pp. 10–14.—Solereder, Holzstruktur, 1885, pp. 56, 57.—O. Bachmann, Schildhaare, Flora 1886, separate copy, pp. 28, 29.—Radlkofer, Sitz.-Ber. Münch. Akad. 1890, p. 306.—Borodin, Krystall. Ablag. in den Bl. der A. etc., Arb. Petersburg. Naturf.-Gesellsch., Bot., 1891, pp. 177–205, Russian; abstract by Rothert, Bot. Centralbl. 1893, ii, p. 51.—H. Schenck, Anat. d. Lianen, 1893, p. 59.—Spencer-Moore, Matto Grosso Exped. 1891–2, Transact. of Linn. Soc., vol. iv, part 3, 1895, pp. 297 and 302 et seq. and pl. 38.—(See also Prantl, in Natürl. Pflanzenfam., iii. Teil, Abt. 2, p. 25.)

MENISPERMACEAE.

1. Review of the Anatomical Features. In all the Menispermaceae, broad primary medullary rays separate the vascular bundles of the axis from one another. In the pericycle there is always an undulated composite and continuous sclerenchymatous ring, which is composed of the arcs of primary hard bast, belonging to the separate vascular bundles, and of groups of stone-cells situated between them. The xylem is characterized by vessels with wide lumina and simple perforations, and by wood-prosenchyma with bordered pits. Bast-fibres are never present in the secondary bast. Spherical secretory cells are absent; but elongated secretory sacs are present in the axis and in the petiole in certain members of the Order (species of *Anamirta, Burasaia, Cissampelos, Diploclisia, Jateorhiza, Limacia,* and *Tinospora*). In the same way the anomalous structure of the axis, viz. the appearance of rings of vascular bundles (Fig. 8), which are secondary and extrafascicular in origin, is known only in certain cases (species of *Abuta, Anomospermum, Chondrodendron, Cissampelos, Clypea, Cocculus, Pachygone,* and *Pericampylus*). On the other hand the excretion of oxalate of lime in the form of small, sometimes acicular, crystals appears to be characteristic of all the Menispermaceae; in addition to these, however, large solitary crystals and clustered crystals may also occur. The hairs are mostly one- or two-celled (in the latter case provided with a long terminal cell); more rarely they consist of a longer row of cells; in isolated cases (*Jateorhiza*), glandular shaggy hairs with a multiseriate stalk and an ellipsoid, glandular, terminal cell are also found (Fig. 7, *A*). In *Anamirta Cocculus* peculiar epidermal structures (unicellular hydathodes, Fig. 7, *B*), serving for the excretion of water, are developed. Special features occurring in the leaf in certain species are: fibre-like spicular cells, subepidermal mucilaginous layers on the upper side of the leaf, peculiar thickenings, restricted to portions of the cell-wall in the mesophyll, especially in the spongy tissue.

2. Structure of the Leaf. The leaves of those species, the structure of which has hitherto been investigated especially by Blottière and Vesque [1], are usually bifacial in structure; more rarely (*Cocculus Leaeba*) the whole mesophyll consists of palisade-tissue. The **epidermal cells** have straight or wavy lateral walls; in the latter case they sometimes have what are called marginal pits. Gelatinization of individual epidermal cells has not been observed; but on the other hand in numerous Menispermaceae, e.g. *Anomospermum reticulatum*, Eichl., Herr Auer has met with subepidermal layers of mucilage, which arise essentially by gelatinization of the inner membranes of all the epidermal cells within one mesh in the network of veins. The formation of papillae has been observed on the lower side of the leaf of *Menispermum canadense*, and, according to Herr Auer, is also not uncommon elsewhere. Excretion of wax occurs on the lower side of the leaf in a species of *Cissampelos*, of which the name is not given (Vesque). In *Burasaia madagascariensis*, a one-layered **hypoderm** is found on the upper side of the leaf (Blottière). In *Cocculus laurifolius* and *C. carolinus*, according to Vesque, the **stomata** are accompanied by subsidiary cells, which lie parallel to the pore. In other species, e.g. *Cissampelos* and *Menispermum canadense*, to some extent even in *Anamirta Cocculus*, this type is obliterated in the mature leaf. The stomata are usually found only on the lower side of the leaf, but in *Cocculus Leaeba* in about equal numbers on both sides of the leaf. Special features in the **mesophyll** are presented by the sclerenchymatous fibres, which traverse the mesophyll of *Anamirta Cocculus* and *Burasaia madagascariensis*, as well as by the peculiar thickenings of cells in the palisade and spongy tissue, restricted to certain parts of the cell-wall. These have recently been found by Herr Auer in many species, e.g. *Stephania hernandifolia*, Walp.

Cxalate of lime is excreted in the tissues of the leaf and axis, and also in the epidermis, chiefly in the form of small crystals, sometimes of acicular form, many occurring together in the same cell. Of these the latter now and then show transitions on the one hand to fine crystal-sand (e.g. in the pith of *Tiliacora racemosa*, Colebr.), and on the other hand to styloid-like crystals. Structures resembling clustered crystals have been observed in the cortex of *Pericampylus incanus*, Miers, large solitary crystals in the neighbourhood of the bast-fibres (*Aspidocarya uvifera*, Hook. f. et Th., &c.), or in the primary medullary rays of the wood (*Cissampelos Pareira*, L.). Sphere-crystals of an organic substance, not accurately known, are formed, according to G. Kraus and Hansen, in the epidermis of the leaf of *Cocculus laurifolius* after the action of glycerine or alcohol.

The occurrence of **secretory cells** which are much elongated and have yellowish or brownish contents, like gum-resin, and frequently including tannin, is characteristic of the petiole and axis of certain Menispermaceae. These secretory cells were observed by Baillon in *Anamirta*, were erroneously described by Blottière as 'canaux lacticifères,' and are best compared with the well-known tannin-sacs in the pith of *Sambucus nigra*. In the axis these secretory sacs may occur in the pith as well as in the cortex. In the exceptional case of *Diploclisia macrocarpa*, Miers, they are very short in the primary cortex and are arranged in longitudinal rows, while in the pith and bast of the same plant much-elongated secretory sacs are present. The secretory sacs in question have so far been observed by me, by Blottière, and Volkens in the following species: *Anamirta Cocculus*, W. et A., *Burasaia madagascariensis*, *Cissampelos Caapeba*, *Cocculus Leaeba*, DC., *Diploclisia macrocarpa*, Miers, *Jateorhiza palmata*, *Limacia velutina*, Miers, and *Tinospora cordifolia*.

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[1] A new anatomical investigation on the leaf-structure of the Order is being carried out at the present time by Herr Auer in Prof. Radlkofer's Laboratory.

Berberin is stated to occur in *Jateorhiza palmata, Menispermum canadense,* and *Coscinium fenestratum.*

The **hairs** may be unicellular (*Abuta rufescens*) or bicellular, and in the latter case (*Cocculus*) they consist of a short, sometimes strongly thickened (*C. Leaeba,* DC.) basal cell and a long, often thin-walled, terminal cell, or they may be multicellular and uniseriate. In *Jateorhiza palmata* slender groups of cells resembling shaggy hairs occur, consisting of several rows of cells with an ellipsoid, glandular, terminal cell (see Fig. 7, *A*).

Amongst the trichomes the unicellular hydathodes (water-absorbing and water-excreting organs) observed by Haberlandt on both sides of the leaf in *Anamirta Cocculus* must also be included. These (Fig. 7, *B*) are rather large epidermal cells of an inverted funnel-shape, and lie at the base of a shallow depression in the leaf-surface. The inner and lateral walls of these hydathodes are not specially thickened, but are lignified. At the centre of the strongly thickened outer wall there is a very peculiar filtering apparatus, which projects outwards in the form of a short membranous papilla, while it is continued inwards as a cystolith-like peg,

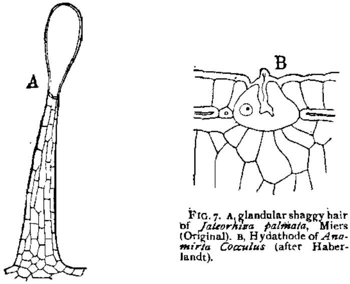

FIG. 7. A, glandular shaggy hair of *Jateorhiza palmata,* Miers (Original). B, Hydathode of *Anamirta Cocculus* (after Haberlandt).

gnarled or with coralloid branches at its extremity. The membranous papilla and the peg are traversed by a delicate filtering-canal, while the papilla at its tip is mucilaginous and is not covered by cuticle.

The **petiole** has been investigated by Plitt and Vesque in *Menispermum canadense* and *Cocculus laurifolius*; in both these plants it contains a circular system of isolated vascular bundles.

3. STRUCTURE OF THE AXIS. In all the Menispermaceae the **vascular bundles** are separated from one another by broad primary medullary rays, and stand out distinctly in a transverse section of the branch.

In certain species (*Anamirta Cocculus,* W. et A., *Coscinium Blumeanum,* Miers, and *Limacia velutina,* Miers), the **pith** exhibits a differentiation into an inner (empty) and an outer active tissue. The latter of these forms a kind of medullary sheath, and, in contradistinction to the isodiametric cells of the inner part, consists of cells which are more strongly elongated in the vertical direction, are provided with slit-like pits, and are sometimes septate by means of thin cross-walls. In other species this kind of differentiation of the pith is wanting, and then (e.g. in *Aspidocarya uvifera,* Hook. f. et Th. or *Cocculus laurifolius,* DC.) groups of cells resembling bast-fibres are frequently present on the inner side of the masses of primary xylem (Eichler's 'innerer Hartbast,' which, however, is not so generally distributed as Eichler supposed).

The primary medullary rays of the **wood** are either lignified, as in *Anamirta*

Cocculus, or unlignified as in *Aspidocarya uvifera*, *Cissampelos Pareira*, and *Menispermum canadense*. The parenchyma of the primary medullary rays sometimes becomes sclerosed between the masses of bast and the adjoining outermost part of the primary medullary rays of the xylem (*Anamirta Cocculus*, *Coscinium Blumeanum*).

The xylem of the vascular bundles occasionally contains narrow secondary medullary rays and a little wood-parenchyma. The xylem consists chiefly of vessels with large lumina (maximum diameter ·3 mm.), and of wood-prosenchyma with bordered pits. The vessels possess simple perforations, and have bordered pits even where in contact with parenchyma.

In young branches, such as are found in herbarium-material, the phloem-portions of the vascular bundles are limited on the outer side towards the primary cortex by crescents of hard bast-fibres. These crescents of hard bast are, moreover, united by intermediate groups of stone-cells into a composite and continuous, undulated ring of sclerenchyma, which I have observed to be constant in the numerous Menispermaceae [1], in which this point has been investigated. This ring is still present in thick axes of *Cissampelos Pareira* and *Hyperbaena domingensis*, Benth., though here the arc-shaped hard bast is split up into groups and the latter are united by stone-cells. In many cases (e.g. in species of *Cocculus*, *Cyclea*, *Peraphora*, *Stephania*, and *Nephroica*) the arcs of hard bast are not in immediate contact with the soft bast on their inner side, but large-celled, unlignified parenchyma intervenes, in which no sieve-tubes occur (parenchymatous pericycle). The secondary bast never contains bast-fibres in this Order. In the **primary cortex** groups of stone-cells are sometimes present (*Anamirta Cocculus*). With regard to the cork very little is known. *Menispermum canadense* is mentioned by De Bary among those plants in which periderm-formation does not occur until a late stage. With regard to the origin of the cork in *Menispermum canadense*, Möller states that it originates superficially in places, at first on circumscribed areas of the stem, and then spreads peripherally, as it penetrates deep into the cortex (compare also Volkens, Taf. 1, Fig. 1); the periderm-cells are small and have delicate walls.

The deposits of crystals and the occurrence of secretory sacs in the axis have already been discussed above.

To conclude the description of the axis it remains to be mentioned, that in certain but not in all the members of the Order an **anomalous stem-structure** occurs in thicker parts of the axis; in these cases a transverse section shows several concentric rings of vascular bundles, which either encircle one another completely on all sides of the transverse section or only develop strongly on one side (Fig. 8). The history of the origin of these anomalously constructed portions of the axis is shortly as follows. Originally only a single normal ring of vascular bundles is present, and its ring of cambium is for some time active in the normal way. Then the activity of this cambium ceases, and an extra-fascicular meristem, which is annular or arc-shaped and only developed towards one side, arises in the innermost part of the primary cortex, which is rich in starch. This cambium at first increases the mass of the primary cortical tissue. In the newly formed tissue secondary procambial strands arise, and from these a second ring or arc of vascular bundles is formed and likewise grows in thickness for some time by means of its normal cambium; on its outer side a ring or arc of stone-cells develops. Outside this ring of stone-cells a second meristem subsequently arises and produces a third ring or arc of vascular bundles and

[1] Species of the following genera were examined by me: *Abuta*, *Anamirta*, *Anomospermum*, *Antitaxis*, *Antizoma*, (*Dissopetalum*), *Aspidocarya*, *Calycocarpum*, *Chasmanthera*, *Chondrodendron*, *Cissampelos*, *Cocculus*, *Coscinium*, *Cyclea*, *Disciphania*, *Hyperbaena*, *Jateorhiza*, *Limacia*, *Lophophyllum*, (*Peraphora*), *Menispermum*, *Pachygone*, *Parabaena*, *Pericampylus*, *Pycnarrhena*, *Sciadotenia*, *Stephania*, *Sychnosepalum*, *Tiliacora*, *Tinospora*.

a second ring or arc of stone-cells bounding the vascular bundles externally. It is worthy of note that the secondarily formed vascular bundles possess no crescents of hard bast and contain no primary forms of vessels (spiral and annular vessels).

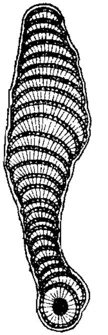

FIG. 8. Anomalously constructed stem of *Anomospermum grandifolium*, Eichl. —After H. Schenck.

The anomaly in question has hitherto been observed in the following Menispermaceae, the name of the authority for the observation being added in brackets: *Cocculus laurifolius* (Decaisne, Eichler, Hérail, Blottière), *C. Leaeba* (Krüger); *Chondrodendron platyphyllum* (H. Schenck), *C. tomentosum* (Blottière); *Pericampylus incanus*, Miers (H. Schenck); *Anomospermum Schomburgkii*, Miers (H. Schenck), *A. grandifolium*, Eichl. (H. Schenck); *Pachygone domingensis*, Eichl. (Witte, Solereder); *Abuta amara* (Blottière[1]), *A. concolor*, Poepp. et Endl. (Solereder), *A. Imene*, Eichl. (Solereder), *A. rufescens*, Aubl. (Aublet, Jussieu), *A. Selloana*, Eichl. (H. Schenck[2]). It is worth mentioning that among the species named, there are not only lianes, but also a tree, *Cocculus laurifolius*.

Those species which possess successive rings of vascular bundles in the axis appear also to have them universally in the root. According to Nägeli this holds good for *Cocculus laurifolius*, according to Blottière for *Abuta rufescens* and *Chondrodendron tomentosum*. The same anomalous structure is also possessed by the root of *Cissampelos Pareira*, L., according to Wigand, and by that of *Clypea Burmanni*, according to Blottière.

Even if in the future a further series of Menispermaceous lianes with anomalous wood should be met with, it is nevertheless to be gathered from present observations, that lianes of normal structure also occur in the Order. As examples of this H. Schenck cites species of the genera *Anamirta*, *Cissampelos*, *Cocculus*, *Coscinium*, *Menispermum*, and *Tinospora*, on the authority of Decaisne, Gamble, Hérail, and Eichler. The root of *Jateorhiza palmata*, Miers (*Radix Colombo*), which has normal growth, is also normal in structure.

Literature: Decaisne, Lardizabalées, Arch. du Mus. d'hist. nat., t. i, 1839, p. 143, tab. x, fig. 18. —Jussieu, Malpighiacées, Arch. Mus. d'hist. nat., t. iii, 1843, p. 125.—Wigand, Flora 1856, p. 676 and Taf. vii.—Radlkofer, Flora 1858, pp. 193–206.—Nägeli, Beitr. z. wiss. Bot. i, 1858, pp. 16–19.—Eichler, Denkschr. Regensburg. bot. Gesellsch., Bd. v, Heft 1, 1864.—Eichler, Flora brasil., vol. xiii, 1, 1864, p. 207 et seq., and Tab. l, li.—Baillon, Adansonia, t. ix, 1868–70, p. 378, see also Hist. des pl., t. iii, 1872, p. 26.—G. Kraus, Pringsheim Jahrb., Bd. viii, 1872, pp. 421–6 and Tab. xxxv.—Möller, Holzanatomie, Denkschr. Wiener Akad. 1876, pp. 68, 69 and 364, 365.—De Bary, Vergl. Anat., 1877.—Gamble, List of the trees, &c. in the Darjeeling district, Bengal, Calcutta, 1878, p. 4. —Vesque, Nouv. Arch. du Mus. d'hist. nat., sér. 2, t. iv, 1881, pp. 44–7 and pl. 2.—Möller, Rindenanatomie, 1882, p. 223.—Hansen, Arb. d. bot. Inst. Würzburg, Bd. iii, 1884, p. 102.—Krüger, Anomale Holzbild., Diss., Leipzig, 1884, p. 23.—Morot, Ann. sc. nat., sér. 6, t. xx, 1885, p. 257. —Hérail, Ann. sc. nat., sér. 7, t. ii, 1885, p. 226.—Mentovich, Mark, Klausenburg, 1885, Hungarian; abstract in Just, 1885, i, p. 789.—Solereder, Holzstruktur, 1885, p. 57.—Blottière, Ét. anat. de la fam. des Ménispermacées, Paris, 1886, p. 7 et seq. and 2 pl.—Plitt, Blattstiel, Diss., Marburg, 1886, p. 13 et seq.—Witte, Lianen, Diss., Freiburg i. Br. and Kiel, 1886, p. 37 et seq.—Volkens, Aegypt.-arab. Wüste, Berlin, 1887, pp. 86–9 and Taf. i, ix and xv.—Prantl, in Natürl. Pflanzenfam., iii. Teil, Abt. 2, 1888, p. 79.—Solereder, Engler, Bot. Jahrb., Bd. x, 1889, p. 482 et seq.—Schenck, Anat. d. Lianen, 1893, pp. 62–70 and p. 252, Taf. ii and iii.—Haberlandt, Trop. Laubbl. ii, Sitz.-Ber. Wiener Akad., Bd. ciii, Abt. 1, 1894, p. 504 (16) et seq. and Taf. ii and Sitz.-Ber. Deutsch. bot. Gesellsch. 1894, p. 369 and Taf. xxiv.—[Schwabach, Bot. Centralbl. 1898, iv, p. 359.]

[1] The anomalous piece of stem in question, described by Blottière as *Abuta amara*, probably does not belong to *Abuta amara*, Aubl., if the latter is really identical with *Aristolochia glaucescens*, H. B. K., as stated in the Kew Index. Without anatomical examination of the branch or leaf, this latter statement, however, appears to me to be not yet quite certainly proved, as Aublet's example is sterile, and Aublet (Pl. de la Guyane franç., i, pp. 620, 621) says of the wood: 'le bois est jaunâtre, formé de plusieurs cercles concentriques.' Or, in the case of the identity of *Abuta amara*, Aubl., with the species of *Aristolochia* mentioned, may the anomaly of successive rings of wood and bast occur in *Aristolochia* also?

[2] It must probably be regarded as an error that H. Schenck (loc. cit., p. 63) quotes *Burasaia madagascariensis* and *Chasmanthera palmata* among the Menispermaceae of anomalous structure, according to Blottière: in Blottière's treatise I find no statement to warrant this.

BERBERIDEAE.

1. Review of the Anatomical Features. There are only a few characters applying generally to the whole Order. Such are, for the woody genera, the occurrence of broad primary medullary rays and the almost exclusive presence of simple perforations in the vessels; further, as concerns the leaf-structure, the absence of special subsidiary cells in the stomatal apparatus and the lack of special internal and external glands. Berberin is frequently found, and gives a yellow coloration to the tissues. The hairy covering consists of simple, unicellular or uniseriate trichomes; in the latter case the hair is composed of two or three short basal cells and a long terminal cell. Oxalate of lime occurs in the form of solitary and clustered crystals. The remaining anatomical features are mostly only of importance for generic and specific diagnosis. Among these are the sub-papillose or papillose differentiation of the lower epidermis of the leaf (species of *Akebia* and *Mahonia*), the occurrence of hypoderm (*Holboellia*) or of sclerenchyma-fibres (species of *Mahonia*) beneath the epidermis on the upper side of the leaf, the spiral thickening of the walls of the vessels and tracheides, the nature and pitting of the wood-prosenchyma (simply-pitted and septate in *Berberis*, simply-pitted also in *Holboellia* and *Nandina*, with bordered pits in *Lardizabala*, &c.). The transverse section of the stem in *Diphylleia*, *Jeffersonia*, *Leontice*, and *Podophyllum* (Fig. 10) shows

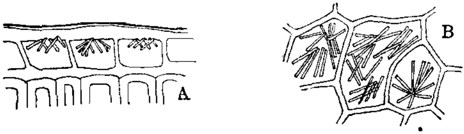

FIG. 9. A–B, Crystals of organic nature in the upper epidermis of the leaf of *Mahonia japonica* (after Vesque).

the same arrangement of vascular bundles as in a Monocotyledonous stem. The cork arises in *Berberis* immediately on the inner side of a zone of sclerenchyma-fibres forming the outer part of the pericycle, or, as in *Podophyllum* and its allies, subepidermally.

2. Structure of the Leaf[1]. The leaf of the Berberideae is, as a rule, bifacial[2] in structure; the palisade-tissue varies in thickness and differentiation. In *Epimedium* the whole of the leaf-tissue consists of cells of uniform shape. The **epidermal cells** have straight, curved or strongly undulated lateral walls. In *Akebia quinata*, Decne., the epidermal cells on the lower side of the leaf are strongly arched outwards; *Mahonia repens* and *M. trifolia*, Cham. et Schlecht., have distinct papillae on the lower side of the leaf; these are found also in the groove of the leaf of *Berberis empetrifolia*, in this case with transitions to unicellular hairs. *Berberis Knightii* has parallel striation of the cuticle, and *Lardizabala triternata* possesses cuticular beads. Hypoderm occurs locally below the epidermis on the upper side of the leaf in *Holboellia latifolia*. Strengthening of the epidermis of a different kind is possessed by certain species of *Mahonia*, e.g. *M. japonica* and *M. trifolia*, as well as by *Berberis empetrifolia*, for in these plants two or more layers of sclerenchyma-fibres, running parallel with

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[1] Chiefly, according to Vesque, in Nouv. Arch. du Mus. d'hist. nat.

[2] The leaf of *Berberis empetrifolia*, Lam., is a rolled leaf with the groove downwards (see Goebel, loc. cit.).

one another, are found below the epidermis; similar bundles of fibres form the margin of the leaf of *Epimedium*. The **stomata** occur only on the lower surface of the leaf, and are surrounded by three or more epidermal cells not distinguished by their form.

The **midrib** of the leaf contains a varying number of vascular bundles, which are surrounded by a sheath of sclerenchyma-fibres. This sheath reaches to the epidermis either on the upper side only or on both sides. The individual bundles of the **petiole**, which, according to Vesque and others, are arranged either in an arc or in a more or less distinct ring, are also usually accompanied by sclerenchyma-fibres, but not always, as is shown by *Akebia*, *Lardizabala*, and *Holboellia*.

Oxalate of lime occurs in the form of solitary or clustered crystals. Besides crystals of oxalate of lime, other components of the cell-contents have been observed in the Order, and should be shortly referred to. Firstly, in most of the cells of the upper epidermis of the leaf in some species of *Mahonia*, e.g. *M. japonica*, *M. tenuifolia*, and *M. Fortunei*, Vesque has observed yellowish or greenish, prismatic crystals of an organic substance, of the chemical nature of which nothing further is known (Fig. 9, *A–B*); these are fixed by one end in groups in the outer wall of one and the same epidermal cell, and project from there into the lumen of the cell in a radiating manner. In the medullary cells of the petioles and secondary petioles of *Lardizabala*, the same author has discovered another body in the cell-contents in the form of superficially wrinkled globules; these bodies are colourless, hard, brittle, insoluble in alcohol and in hydrochloric acid, and are not stained by iodine solution (i.e. probably silica ?). Lastly, in the chloroplasts of the palisade-tissue of *Berberis vulgaris*, Zimmermann met with acicular or apparently triangular crystalloids. In connexion with these special components of the cell-contents, it should also be stated that true secretory-receptacles are absent. But it is nevertheless worthy of remark, that resinous substances are stated to occur in the rhizome of *Podophyllum*; further, that the yellow coloration of the tissues of *Berberis* and of the root of *Jeffersonia* is caused by berberin, which may also be recognized as golden-yellow contents in the ray-parenchyma of the bast in *Berberis*; and lastly, that berberin is also present in *Podophyllum peltatum*, L., in *Leontice thalictroides*, L., and in *Nandina domestica*, Thunb.

The **hairs** of the Berberideae are simple; they are either unicellular (*Podophyllum Emodi* and *Diphylleia Grayi*), or consist of a row of cells, which is formed of a variable number of short basal cells and a long terminal cell filled with yellowish or brown contents (*Epimedium niveum*, *Lardizabala triternata*). True glandular hairs have not been observed in the Order.

3. Structure of the Axis. In the genera with a strongly developed mass of **wood** (*Berberis*, *Nandina*, *Lardizabala*, *Holboellia*, and also in *Akebia*), broad primary medullary rays separate the individual vascular bundles from one another. These primary medullary rays do not become closed by interfascicular wood, but form longitudinal plates which split up the wood into longitudinal segments. The vessels have lumina of varying size (maximum diameter, ·036 to ·093 mm.) and their arrangement is also variable; their cross-walls, as a rule, are provided with simple perforations, more rarely they are scalariform, with few bars (*Berberis*, *Holboellia*). The occurrence of spiral thickening of the wall together with bordered pits in the vessels with smaller lumina, and in the tracheides of *Berberis*, *Nandina*, and *Holboellia*, is worthy of note; in *Lardizabala biternata*, Ruiz et Pav., this is only slightly indicated. The wood-parenchyma is little or not at all developed. With regard to the pitting of the wood-prosenchyma differences are found in the Order. Thus the wood-prosenchyma of *Berberis* is simply-pitted and the lumen of these elements is sometimes provided with a few delicate cross-walls; in *Holboellia*

and *Nandina* simply-pitted prosenchyma also occurs apart from the tracheides with bordered pits and spiral thickenings; in *Lardizabala* prosenchyma with bordered pits alone appears to be present.

Concerning the remaining genera of the Order it must be pointed out that in *Podophyllum* (Fig. 10), *Jeffersonia*, *Diphylleia*, and *Leontice*, the **vascular bundles** exhibit an irregular scattered arrangement in the transverse section of the stem, similar to what is found in a Monocotyledon. That is to say, around a pith, which in *Leontice* is subsequently replaced by a cavity, parenchymatous ground-tissue is found, in which numerous vascular bundles are irregularly scattered. The outermost of these in *Podophyllum* have their bast-portions embedded in a ring of sclerenchyma. The vascular bundles in question, which are scattered in the transverse section, are without doubt of the nature of leaf-traces; their course has, however, not yet been investigated in detail.

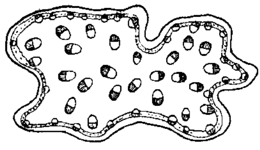

FIG. 10. Diagrammatic transverse section through the stem of *Podophyllum peltatum*, L. (Original, from herbarium-material; the phloem of the vascular bundles shaded, the xylem blank.)

Our knowledge of the structure of the **cortex** practically extends only to the genus *Berberis* (including *Mahonia*). In this plant the pericycle is formed, in its outer part, by a broad ring of sclerenchyma-fibres with wide lumina, and in its inner part of many-layered parenchyma. In the outermost layer of cells of the latter, cork-cells with wide lumina and delicate walls appear even in the first period of vegetation. *Berberis vulgaris* (unlike *Mahonia*) possesses secondary hard bast. This is formed of yellow-walled sclerenchymatous fibres, resembling rod-cells and occurring singly in the outer part of the phloem, but in tangential rows in the inner part. According to Douliot's researches the cork in *Podophyllum*, contrary to the case of *Berberis*, arises subepidermally, and according to Prantl this is quite general in the 'Lardizabalaceae[1]'; where a composite and continuous ring of sclerenchyma is present in the pericycle.

The **pith** has likewise only been investigated in *Berberis* (including *Mahonia*) by Gris. It is worthy of note that *Berberis vulgaris*, *B. macrophylla*, *B. nepalensis*, and *B. sinensis* possess a heterogeneous pith, while *Mahonia aquifolium* has a homogeneous pith. The heterogeneous pith of *Berberis vulgaris*, &c. is formed by a centrally placed cylinder of empty cells with large cavities and thin walls, while its peripheral part is composed of thicker-walled, active cells.

As regards the structure of the **root** it need only be mentioned, that its cortical parenchyma exhibits ridge-like thickenings of the walls in *Mahonia aquifolium*.

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[1] The 'Lardizabalaceae' of Prantl are formed by the genera *Decaisnea*, *Stauntonia*, *Holboellia*, *Parvatia*, *Akebia*, *Boquila* and *Lardizabala*.

d. Stammes der Berberitze, Diss., Königsberg, 1885.—Solereder, Holzstr., 1885, p. 60.—Plitt, Blattstiel, Diss., Marburg, 1886, pp. 12, 13.—Prantl, in Natürl. Pflanzenfam., iii. Teil, Abt. 2, 1888, pp. 67 and 71.—Douliot, Ann. sc. nat., sér. 7, t. x, 1889, p. 334.—Lalanne, Feuilles persist., Act. Soc. Linn. *Bordeaux*, sér. 5, t. iv, 1890, pp. 34 and 104, pl. vi.—J. E. Weiss, Denkschr. Regensb. bot. Gesellsch., Bd. vi, 1890, separate copy, p. 67.—Goebel, Pflanzenbiol. Schild. ii, Lief. 1, 1891, p. 25 and Taf. xii.—Zimmermann, Pflanzenzelle, 2. Heft, 1891, p. 149.—H. Schenck, Anat. d. Lianen, 1893, pp. 61, 62.—[Bastin, Structure of *Podophyllum*, Americ. Journ. of Pharm. 1894.]

NYMPHAEACEAE.

1. Review of the Anatomical Features. The following anatomical features are characteristic of all the Nymphaeaceae: the closed vascular bundles of the stem, which, in a transverse section, are for the most part irregularly arranged, as in the Monocotyledons; the occurrence of numerous air-spaces; the abortion of the primary xylem-groups of the vascular bundles in consequence of the secondary appearance of air-passages; the lack of true vessels; further, the bifacial structure of the leaf; the restriction of the stomata to the upper surface of the leaf; the absence of special subsidiary cells

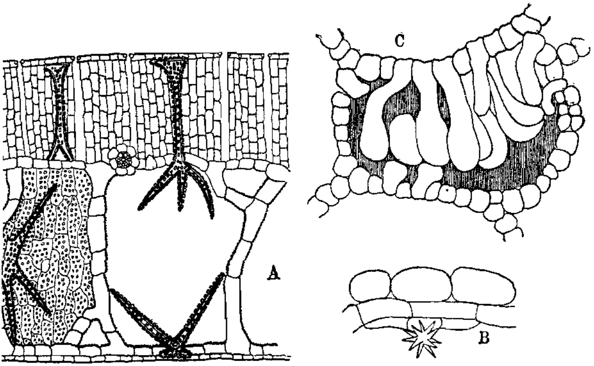

Fig. 11. *A*, Transverse section through the leaf of *Nymphaea Marliacii*, Hort.; the crystals in the walls of the picular cells and of the spongy parenchyma are drawn larger than they are in reality. B, Transverse section hrough the wall of an air-passage from the petiole of *Nelumbium speciosum*, Willd., with a cell bearing clustered crystal. C, Intercellular space of *Brasenia peltata*, Pursh., filled with mucilage-hairs. A–B, Original. , After Schrenk.

accompanying the guard-cells; the occurrence of laticiferous sacs; finally, the uniform nature of the hairy covering, the latter being composed of (*a*) simple few-celled mucilage-hairs, which consist of two short stalk-cells and a short or longish terminal cell, secreting mucilage (Fig. 12, *B–F*), and (*b*) clothing hairs, which are likewise uniseriate. In some of the genera the deposition and embedding of small crystals of oxalate of lime on or in the walls of ordinary or of specially shaped cells has been observed; whether this obtains in all Nymphaeaceae has yet to be decided. As an anatomical characteristic of certain genera the following features should be pointed out: the presence of branched sclerenchyma-cells with their arms projecting into the lacunae (in

Nymphaea, Fig. 11, A, *Nuphar*, *Victoria*, and *Euryale*); the occurrence of clustered crystals (in *Nelumbium*); and finally, the varying differentiation of the laticiferous sacs and of the vascular system (simple vascular bundles, double vascular bundles, or vascular system of polystelic structure, see below).

2. Structure of the Leaf. The mesophyll is bifacial in structure. The spongy tissue is distinguished by having wide intercellular spaces. The **stomata** are found only on the upper surface of the leaf[1] in all cases, even when the leaves are raised above the surface of the water, as in *Nelumbium*, in *Nuphar advena*, and in the land-forms. The guard-cells of the stomata are surrounded by epidermal cells, which are not of special form, and are irregularly placed. In *Nelumbium speciosum*, Willd., there is a group of water-pores at the centre of the upper side of the leaf. Water-pores also occur on the peltate leaves of *Brasenia peltata*, Pursh., at the points of junction of the anastomosing veins. The **epidermal cells** usually have almost straight, more rarely undulated lateral walls; in *Nelumbium* the upper epidermis is papillose. The smaller veins of the leaf are embedded in the mesophyll, and are without sclerenchyma. The latter is also absent in the larger veins and in the petiole.

Peculiar **branched sclerenchymatous cells** (so-called internal hairs, Fig. 11, *A*) occur in the tissue of the leaf and in other parts of the plant in *Nymphaea*, *Nuphar*, *Victoria*, and *Euryale*, but not in *Cabomba*, *Nelumbium*, and *Brasenia*; the arms of these cells project into the lacunae. These sclerenchyma-cells are sometimes (*Nymphaea*, *Nuphar*) covered externally with small knobs, which can be shown to be due to a deposition of small crystals of calcium oxalate in the cell-wall (Schenck, Kohl). In *Nymphaea* and *Nuphar*, also in *Nelumbium* according to Kohl, and in *Brasenia* according to my own observations, the walls of the parenchyma, which border the air-spaces, are also covered with exactly similar small crystals; these latter, however, are not embedded in the cell-wall, but are rather deposited on it (Molisch, Kohl).

Apart from the smaller crystals just described, **oxalate of lime** has only been observed in *Nelumbium*, and here in the form of clustered crystals in the stem, in the petiole (Fig. 11, *B*), and in the lamina of the leaf. These clustered crystals are contained in small cells, which in shape are completely adapted to their contents; they occur only in the partition-walls of the lacunae, and project into the latter like hairs. It may be added that in the tissue of living subterranean rhizomes of *Brasenia*, Raciborski has discovered large, yellow, rhombic crystals, which consist of a substance (brasenin), probably belonging to the series of fats, but not accurately known, and that in the palisade-tissue of *Nuphar advena* Zimmermann has observed crystalloids, which lie in the cell-sap.

The **secretory elements** of the Nymphaeaceae, which were described by Vesque, though with some reserve, as articulated laticiferous tubes, and which had already been seen, previous to Vesque's observation, by Trécul and Wigand, are, according to the more recent researches of Van Tieghem, only laticiferous sacs. They are quite generally characterized by a thin, but suberized cell-wall, and are found in the vegetative organs, as well as in the peduncle, of all the Nymphaeaceae, both in the parenchymatous ground-tissue and in the wood and bast of the vascular bundles. The varied differentiation of the laticiferous sacs is characteristic for the different tribes of the Order. *Nuphar* (Nuphareae) possesses laticiferous sacs, which are nearly isodiametric, only those in the tissue of the bundles being elongated; they are mostly placed singly, and only rarely in twos or threes one above another. The same

[1] According to Goebel stomata are absent on the submerged simple leaves of *Nuphar* and on the divided leaves of *Cabomba*. On the other hand, stomata were found by him on the permanently submerged primary leaves of *Nymphaea coerulea*.

applies to *Nelumbium*. On the other hand, in the Cabombeae (*Brasenia, Cabomba*) many laticiferous sacs are associated together in long rows. Finally, the Nymphaeaceae (*Nymphaea, Victoria, Euryale*) again possess laticiferous sacs, which are isolated or only occur superposed in small numbers; they are distinguished from those of all other Nymphaeaceae by their tubular shape and their considerable length (up to 2 cm. and more).

The **hairy covering** is usually present only on the young organs, especially in the bud-stage, and, as a rule, is subsequently lost. According to Schilling it consists of two kinds of trichomes, viz. clothing hairs and mucilage-hairs. The long clothing hairs, which have been investigated in *Nuphar luteum*, Sibth. et Sm. (Fig. 12, *A*), *Nymphaea alba*, L., *Euryale ferox*, Salisb., and *Victoria regia*, Lindl., are formed by a row of cells, of which the lowest two to three are short, and have their longitudinal walls suberized. The structure of the mucilage-secreting, glandular hairs differs. The mucilage-hairs of *Brasenia peltata*, Pursh (Fig. 12, *B*), *Cabomba aquatica*, Aubl. (Fig. 12, *C*), *Euryale ferox*, Salisb., and *Victoria regia*, Lindl., agree in springing from an epidermal cell, which differs from the neighbouring cells by its smaller size, and in consisting of a basal part of two cells with their longitudinal walls suberized (but not their cross-walls), and of a longer, mostly club-shaped end-cell, which secretes mucilage beneath its cuticle. The terminal cell, moreover, is of spherical form in *Cabomba aquatica*, while in *Brasenia peltata* it is sometimes emarginate and appears forked at its extremity. The mucilage-hairs of *Nuphar luteum*, Sibth. et Sm. (Fig. 12, *D*), have an essentially different structure; on the basal cell, which is situated in the plane of the epidermis, and in this case also is distinguished from the neighbouring cells by its smaller size, there is inserted a shortly ellipsoid body consisting of three short cells; of these the lower two have their longitudinal walls suberized and must be called basal cells, while the upper cap-shaped cell alone excretes mucilage. The mucilage-hairs of *Nymphaea alba*, L., and other species of this genus (Fig. 12, *E–F*) are raised still less above the surface of the organ than those of *Nuphar luteum*. The epidermal cell, which serves as the base of the mucilage-hair, and the two adjoining short basal cells (which latter are provided with suberized walls) are sunk in the surface of the organ so that only the short cap-shaped, secretory, terminal cell is raised above the surface. *Nelumbium* has no mucilage-hairs. Mucilage-formation similar to that of the mucilage-hairs just described is sometimes also exhibited by tylosis-like hair-structures, which not uncommonly occur inside the intercellular spaces of *Brasenia* (Fig. 11, *C*) according to Schenck, and occur in *Nymphaea* according to Mellinek; in *Nuphar* they quite generally produce false diaphragms (see below) according to Trécul.

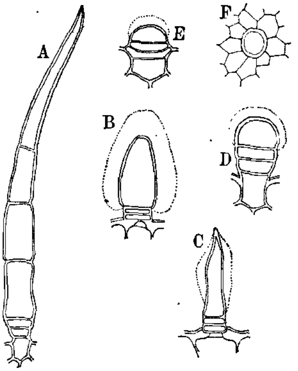

FIG. 12. Hairy covering of the Nymphaeaceae. A, Clothing hair of *Nuphar luteum*, Sibth. et Sm. B–F, Mucilage-hairs: B, *Brasenia peltata*, Pursh; C, *Cabomba aquatica*, Aubl.; D, *Nuphar luteum*, Sibth. et Sm.; E–F, *Nymphaea alba*, L.—A–E, after Schilling; F, original.

With regard to the **spines** of *Euryale*, which, according to Arcangeli, occur in four forms, it may be mentioned that the fibro-vascular tissue sometimes takes part in their formation, and with regard to the depressions at the tips of the spines of *Victoria*, described by Trécul as 'osteola,' it may be stated that according to Raciborski they represent the scars of mucilage-hairs, which have fallen off. Lastly, the occurrence of transparent dots on the leaves of *Victoria* should also be dealt with. According to Unger, Blenk, and Raciborski, they are due to somewhat sharply bounded pits, which always run towards one another from opposite sides of the leaf. The formation of these pits is due to the dying off and collapse of a group of cells of the leaf-tissue in the region concerned, at a time when complete extension of the cells of the leaf-tissue has not yet taken place. It is also of interest, that the masses of dead tissue become, as it were, cut off from connexion with the living cells of the leaf-tissue, since the neighbouring cells become completely grown together and thus close the intercellular spaces towards the attenuated areas of the leaf. The physiological significance of these pits (with regard to this see also Sachs, Flora, 1893, p. 61, and Raciborski) has not yet been fathomed. Further, it may be remarked that in old leaves the pits are often filled with Algae and with a deposit of lime.

3. STRUCTURE OF THE AXIS. In the Nymphaeaceae, as in all water-plants, we meet with an abundant system of intercellular spaces in the axis. The intercellular spaces arise schizogenously and are sometimes provided with a peculiar clothing membrane, which is termed a cuticle by Frank, but according to Raciborski has proved to be a mucilaginous substance free from proteid. The arrangement of the air-passages in transverse section varies. In *Nymphaea*, *Victoria*, and *Euryale*, the intercellular spaces are arranged in circles, are separated from one another by multiseriate bridges of tissue, and are traversed by true tissue-diaphragms. In *Nuphar*, on the other hand, they have a more reticulate distribution; the bridges of tissue between them are only uniseriate, and true diaphragms are absent. In place of the latter, false, loosely constructed diaphragms are found in *Nuphar*, as Trécul had already observed; these arise as follows: the cells forming the walls of the intercellular spaces grow out into internal hairs, which branch dichotomously and secrete mucilage, and the contiguous walls of these hairs then stick together.

In the arrangement of the **vascular bundles** in the stem the members of this Order recall the Monocotyledons. The vascular bundles, which are present in smaller or larger number, are generally arranged in an irregular manner in the transverse section; cambial activity is wanting. As regards the structure of the vascular bundles, it should be mentioned, that true vessels do not occur (Caspary); the spirally and annularly thickened elements, which attain a considerable length (sometimes 5 inches), are only tracheides. These tracheides are commonly destroyed by the formation of schizogenous air-passages, as in other water-plants and in the Monocotyledons, so that the vascular bundle then often consists only of the intercellular passage and a bundle of phloem. Sclerenchymatous elements are not differentiated in the vascular bundles. Only *Nelumbium* possesses a sclerenchymatous bundle-sheath (Van Tieghem). The double vascular bundles, present in certain Nymphaeaceae and in certain organs, arise by the confluence of two vascular bundles with their xylem-groups directed towards one another; a polystelic vascular system arises by the union of more than two vascular bundles into a group, in which case also the xylems are directed towards one another.

According to Van Tieghem double vascular bundles occur exclusively in the rhizome and petiole of *Brasenia* and *Cabomba* (Cabombeae), while in the peduncle the (three) vascular bundles are simple, normally orientated, and arranged in the form of a regular triangle. In *Nuphar* and *Barclaya* double vascular bundles are absent; in the rhizome, petiole and peduncle, only isolated simple vascular bundles with normally orientated wood and bast occur. The vascular bundles show similar features in the rhizome of *Euryale*, *Victoria*, and usually also (see Gwynne-Vaughan)

of *Nymphaea*, while in the petiole and peduncle of these genera double vascular bundles as well as simple normally orientated bundles are developed. Lastly, *Nelumbium* has in its rhizome petiole and peduncle two kinds of simple vascular bundles, the one kind normally, the other inversely orientated, the latter having the phloem inwards.

In connexion with this the following points should also be mentioned as to the position of the double vascular bundles in the Cabombeae. A transverse section of the internode shows the vascular system in the form of two arcs, which are convexly curved on the outer side and each enclosed by a separate endodermis (these are the double bundles). Each of these arcs consists of two vascular bundles fused by means of their xylem-groups, which occupy the middle portion of the arc, while each of the flanks of the arc is occupied by one of the two phloem-groups. The contiguous primary xylem-groups of the two fused vascular bundles in the middle of the arc are replaced by a cavity (see above). In the node each arc resolves itself into two vascular bundles. With regard to the further course of the bundles it is sufficient here to refer to Van Tieghem. On the other hand it may be added, that the petiole contains a double vascular bundle, which corresponds in shape with an arc of the vascular system of the internode of the stem.

Polystely has been found by Gwynne-Vaughan in the primary stolons of *Nymphaea flava* and *N. tuberosa*.

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SARRACENIACEAE.

The anatomical features of this biologically interesting Order of plants will only be discussed here in so far as corresponds with the object of this book. For the remaining facts the literature cited may be referred to.

The ascidiform leaves give a characteristic appearance to the whole Order. According to Goebel's investigations the entire leaf-rudiment, with the exception of a lower portion of it, takes part in the formation of these ascidia. Their anatomical structure is best known in *Sarracenia*, in which the pitchers possess a lid-like terminal part shaped like a standard. The outer side of the tube shows little that is noteworthy; in the chlorophyll-bearing epidermis stomata are found; further, glands occur here, which will be described more fully below,

and small scattered hairs are found. On the inner surface of the tube (Fig. 13, *A*) four zones are clearly distinguished. Firstly, the 'glandular zone' (*a*), which occupies the inner part of the lid; in this the chlorophyll-containing epidermis includes stomata, and bears long unicellular hairs, which are directed downwards, and filled with air, and appear longitudinally striated in consequence of the

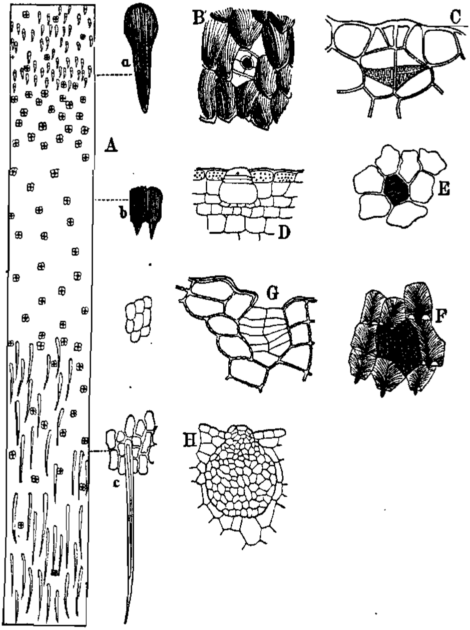

FIG. 13. Anatomical features of the genera *Sarracenia*, *Darlingtonia* and *Heliamphora*. A, Diagrammatic view of the inner wall of the pitcher of *Sarracenia variolaris*. B, Gland of *Sarracenia* from the slippery zone in surface-view. C, Gland of *Sarracenia* in section. D–E and F–G, Glands of *Darlingtonia*. H, Many-celled gland of *Heliamphora nutans*, Benth.—A and D–G, after Macfarlane; B–C, after Goebel; H, after Krafft.

wrinkling of their cell-walls; numerous honey-excreting glands occur here, especially towards the lower limit. The glandular zone is followed by the 'slippery zone' (*b*), which in surface view has the appearance of a tiled roof or a layer of fish-scales (Fig. 13, *B*); that is to say, it consists of cells, the downwardly directed projections of which overlap one another like the tiles of a roof; in this slippery zone, on which no insect can get a foothold, both hairs and stomata are absent, but more or less numerous glands are present. The third zone, of a dull appearance, and occupying the greater part of the tube, is the 'eel-

trap-zone' (*c*), in the epidermis of which are inserted long straight needle-shaped hairs, which spring from an oblique, thick-walled, polygonal or ellipsoid base, and have their points directed downwards; between them glands are also found, but no stomata. The fourth and lowest zone of the tube has a smooth epidermis without glands, stomata, or hairs. Between the slippery zone and the eel-trap-zone still another zone is intercalated in certain species, e.g. *S. purpurea*; it is characterized by its glossiness, and it possesses neither hairs nor stomata, but abundant glands.

The following facts must be mentioned with regard to the structure of the glands in *Sarracenia* (Fig. 13, *B–C*). They are in general spherical, with a neck-like narrowed part directed outwards, and are thus roughly of the shape of a laboratory flask with a short neck; they belong to the leaf-tissue itself, and are not differentiated as hairs. In the plane of the epidermis they consist of six cells; of these the two central ones, which are narrowed inwards like wedges, appear semicircular or rounded-triangular, when seen from the surface, and resemble guard-cells; around them are placed the other four cells. The chief part of the gland lies below the epidermis and consists as a rule of sixteen cells, which are arranged in two tiers, separated from one another by reticulately thickened transverse walls. It should be pointed out that the glands are separated from the remaining tissue by a cuticularized lamella.

The ascidiform leaf of *Darlingtonia* has its upper part arched like a helmet, and bears an appendage like a fish's tail; it shows anatomical features analogous to those of *Sarracenia*. It need only be noted that, apart from the helmet, the whole of the inner side of the tube is destitute of glands. These latter also are much more simply constructed than in *Sarracenia*; in the glands, which in general have the same structure as in *Sarracenia*, the tiers are mostly one-celled, more rarely two- or three-celled (Fig. 13, *D–G*).

In the third genus of the Order, *Heliamphora* (Fig. 13, *H*), which is characterized by ascidiform leaves with a wide opening and a small spoon-shaped appendage, the characteristically constructed slippery zone is wanting according to the descriptions of Goebel, Macfarlane, and Krafft. In the tube of *Heliamphora* an additional and specially remarkable fact is that the eel-trap-zone contains strongly elevated stomata (Krafft). Glands of three kinds are found in *Heliamphora*: firstly, the same kind of glands as in *Sarracenia* on the inner side of the lid-portion (i.e. the upper free part of the pitcher, which adjoins the spoon-shaped appendage) and on the entire outer surface of the ascidiform leaves; secondly, glands of more numerous cells, which are simply glands of the *Sarracenia* type enlarged by cell-division, and occurring in the same regions; thirdly and lastly, large multicellular glands (of several hundred cells) occurring on the inner side of the spoon-shaped appendage (Fig. 13, *H*). According to Krafft, all the glands of *Heliamphora* are developed each from one epidermal cell. With regard to the hairy covering of *Heliamphora*, it must be added that the inner surface of the lid-portion bears conical unicellular hairs with ridge-like thickenings of the wall at regular intervals, which converge towards the tip of the hair, and that on the outer side of the pitchers simple unicellular trichomes occur, some of which are sunk in the epidermis in adjacent pairs.

To pass to the remaining anatomical features of the Order, which come under consideration, it should be mentioned (*a*) that the stomata are not accompanied by any special subsidiary cells [1], (*b*) that the mesophyll is formed for the most part of a spongy tissue, consisting of large chlorophyll-containing cells with large intercellular spaces, a denser small-celled tissue being developed

[1] With regard to the development of the stomata, Vesque states that the mother-cell of the pair of guard-cells is cut off by the first division-wall, as in the Ranunculaceae, and thus coincides with the initial cell.

only immediately below each epidermis, and (c) that the vascular bundles are accompanied on both sides by groups of hard bast, or are enclosed by a ring of bast-fibres. Internal secretory organs have not been observed in any member of the Order.

Excretion of **oxalate of lime** has been met with in the mesophyll of *Heliamphora* only, in the form of clustered crystals (Krafft). Vesque mentions the absence of oxalate of lime in the Sarraceniaceae investigated by him.

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PAPAVERACEAE.

1. Review of the Anatomical Features. The lack of glandular hairs and of special subsidiary cells accompanying the guard-cells is characteristic of the Order; further, the occurrence of simple perforations in the vessels and of wood-prosenchyma with simple pits in the woody species. Secretory organs producing a milky substance are widely distributed in the Papaveraceae; the nature of these organs, i.e. whether articulated laticiferous tubes or only laticiferous sacs, can be employed for characterizing and distinguishing the genera. The scanty hairy covering is formed by multicellular uniseriate simple hairs or by biseriate or multiseriate shaggy hairs. Oxalate of lime has been observed only in *Bocconia*, where it has the form of clustered crystals.

2. Structure of the Leaf. On this subject the following points should be mentioned according to the statements of Vesque and Léger. The **mesophyll** is, as a rule, bifacial in structure. It is of homogeneous nature with more or less distinct development of palisade-tissue in *Papaver somniferum*, L., *Meconella oregana*, Nutt., *M. californica*, Torr., and *Platystigma lineare*, Benth. In *Eschscholtzia californica*, Cham., and *E. tenuifolia*, Benth., palisade-tissue is found on both sides (Léger). The **epidermal cells** have straight or undulated lateral walls. According to Vesque, the epidermal cells of *Glaucium corniculatum* exhibit peculiar thickenings of their lateral walls; according to Léger, the epidermis of the lower side of the leaf is slightly papillose in *Sanguinaria canadensis*, L.; in *Dendromecon rigidum*, Benth., the epidermal cells on both sides of the leaf are produced into conical papillae. A coating of wax is not uncommonly present on the surface of the leaf, e.g. in *Bocconia cordata*, Willd. The **stomata** are surrounded in an irregular manner by several ordinary epidermal cells, and occur either on both sides of the leaf, or only on the lower side. According to Vesque, their development is the same as in the Ranunculaceae. The pair of guard-cells does not always possess the usual elliptical outline; not uncommonly (*Hunnemannia fumariaefolia*, Sweet, *Eschscholtzia californica* and *E. tenuifolia*) the outline is polygonal, according to Léger. In *Papaver somniferum*, *P. orientale* and others, several **water-pores** grouped together are situated on the leaf-teeth in a small hood-like depression of the lower surface of the leaf. The vascular bundles of the smaller veins of the leaf are embedded in the mesophyll, and possess no sclerenchyma.

With regard to the **petiole**, which has been investigated in species of *Bocconia*, *Chelidonium*, *Eschscholtzia* and *Papaver*, it should be stated, that its transverse section in the characteristic region (' caractéristique ') shows isolated vascular bundles arranged in the form of a horseshoe.

Crystalline deposits of oxalate of lime are rare in the Order. They have so far been observed only in *Bocconia frutescens*, where they occur in the form of clustered crystals.

The **hairy covering** is likewise scanty. Firstly, there occur simply uniseriate trichomes (*Chelidonium*, *Glaucium*, *Roemeria*). A special form of these is presented by the hairs found by Léger in *Glaucium luteum*, Scop., which consist of a row of short cells and terminate in a spherical cell, which is, however, not glandular. The uniseriate trichomes of species of *Glaucium* and *Roemeria*, owing to longitudinal division of their lower cells, sometimes show transitions to the biseriate or multiseriate shaggy hairs, which have been observed in species of the genera *Bocconia*, *Meconopsis*, *Papaver*, *Platystemon*, *Platystigma*, and *Roemeria*. These shaggy hairs are very frequently jagged or finely toothed, owing to papillose development of their epidermal cells. Glandular hairs have not been observed in a single member of the Order.

The occurrence of **secretory organs** producing latex is widely distributed in the Papaveraceae. We owe the most recent investigation of them to Léger, who has traced them in the genera *Papaver*, *Argemone*, *Meconopsis*, *Roemeria*, *Platystemon*, *Chelidonium*, *Glaucium*, *Bocconia*, *Sanguinaria*, and *Eschscholtzia*. His voluminous treatise, however, is not wholly satisfactory, as he gives too superficial an account of the morphological nature of the latex-producing elements, without subjecting the better statements of the older literature to a critical examination. Consequently in the following description I prefer to place the results of the older work in the foreground, and to emphasize the fact, that a re-investigation of the latex-producing organs of the Papaveraceae would in no way be superfluous.

The nature of the latex-producing organs varies; they are either true articulated laticiferous tubes (laticiferous vessels), in which the cross-walls and lateral walls may sometimes be furnished with sieve-plates, or they are laticiferous sacs. The secretory elements of *Papaver*, *Argemone*, *Roemeria*, and *Chelidonium* belong to the category of articulated laticiferous tubes, and according to Léger, this probably also applies to those of *Meconopsis* and *Platystemon*; the secretory organs of *Bocconia*, *Glaucium*, *Sanguinaria*, *Eschscholtzia*, and *Hypecoum* are laticiferous sacs. The nature of the secretory elements of *Cathcartia* and *Stylophorum*, in which Bentham and Hooker mention a ' succus flavus,' has still to be determined. Among the articulated laticiferous tubes two types may be distinguished. The first of these is found in *Papaver*, *Roemeria*, and *Argemone*, and consists of tubes, which arise by the fusion of elongated cells. They only rarely have recognizable remains of the cross-walls in the mature condition, and they anastomose more or less abundantly with one another. The second type is represented by *Chelidonium* and is characterized by the fact that the transverse walls are always provided with one or several large perforations in their central region only, while their marginal part is retained; anastomoses are absent. The laticiferous sacs have delicate walls, and are roundish or cylindrical, more or less elongated cells, which either occur isolated or are arranged in longitudinal rows. As regards the position of the laticiferous secretory organs of the Papaveraceae, it need only be briefly mentioned, while referring to Léger for more detailed statements, that these elements belong exclusively to the vascular-bundle-system in *Papaver*, *Argemone*, *Platystemon*, and *Roemeria*, and also in *Meconopsis*, at any rate, in the root and branch, while in the remainder of the genera investigated they are also met with outside the vascular system.

The contents of the laticiferous elements are very diverse, according to Léger and others. They are always milky, opaque, and at the same time white or yellow in colour in *Papaver*, *Argemone*, *Meconopsis*, *Roemeria*, and *Chelidonium*; in the branch of *Platystemon* they are for a time colourless. In *Bocconia cordata* the contents are clear and red at a young stage, and in certain parts of the plant; subsequently they become yellow and turbid. The contents of the secretory organs of *Sanguinaria canadensis* are blood-red but milky. In *Glaucium* the latex is at first clear and red, afterwards golden yellow and turbid; it is just the same in *Eschscholtzia*. In most Papaveraceae (*Papaver*, *Argemone*, *Meconopsis*, *Platystemon*, *Roemeria*, *Chelidonium*, *Sanguinaria*, *Bocconia*) the latex persists during life; in *Eschscholtzia*, on the contrary, it disappears at least in part in the fully grown organs. Lastly, it may also be mentioned here that Scott demonstrated the presence of nuclei in the laticiferous elements of *Chelidonium*; this was the first demonstration of nuclei in articulated laticiferous tubes.

3. STRUCTURE OF THE AXIS. Of the structure of the axis only little is known. De Bary includes *Papaver* among the genera with **medullary bundles**, while the remainder of the Papaveraceae (see Léger) have a simple ring of vascular bundles, between which the interfascicular tissue usually (exceptions: *Dendromecon* and *Hunnemannia*, according to Léger) becomes lignified. The leaf-trace-strands are arranged in several rings in *Papaver*; growth in thickness does not take place in them; their structure is usually collateral, sometimes (*P. umbrosum*, according to Möbius) in part concentric, with central phloem or xylem.

The structure of the **wood** has been investigated in somewhat greater detail in *Bocconia* and *Dendromecon*. The wood of both is characterized by simple perforations in the vessels, by 3–5-seriate medullary rays and by simply-pitted wood-prosenchyma. In *Dendromecon rigidum*, Benth., the pitted vessels, which have rather narrow lumina, are provided with a spiral band. As to the structure of the **cortex**, it should be noted that according to Léger the pericycle is usually sclerenchymatous (exception: rhizome of *Sanguinaria canadensis*), and that the endodermis is scarcely distinct.

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FUMARIACEAE.

The anatomical works dealing with the representatives of this Order (which consists solely of herbaceous plants) are for the most part only concerned with the peculiar **idioblasts or secretory cells**, which are best

denoted (to follow Heinricher's example) by the indefinite name 'sac-cells.' These sac-cells, which form a characteristic feature of the Order, were observed by Zopf in the different vegetative and reproductive organs of numerous species (*Corydalis cava, C. pumila, C. Halleri, C. ochroleuca, C. lutea, Dicentra spectabilis, D. formosa, Adlumia cirrhosa, Fumaria muralis* and *F. officinalis*), and almost simultaneously by Heinricher in the mesophyll of the leaf of *Adlumia cirrhosa*, Raf., *Corydalis rosea*, Zeyh., and *C. capnoides*, Pers. Besides Zopf and Heinricher, Léger also has recently been engaged in a series of investigations on the secretory elements in question. The sac-cells are more or less elongated cells, some of which attain a length of 2–10 mm.; they have colourless or yellow or red contents. They occur in the cortex, in the interfascicular tissue, and in the pith of the branches as well as in the mesophyll. The long cells are found chiefly in the ground-tissue (also in the mesophyll), the shorter cells in the secondary tissue-systems. The long sac-cells are isolated, the shorter ones are sometimes arranged in longitudinal rows. In the latter case, according to Léger, resorption of the separating walls of the sac-cells occurs now and then (*Corydalis*). In this way a closer comparison of the rows of sac-cells with the articulated laticiferous tubes of the Papaveraceae, the nearest allies of the Fumariaceae, would be rendered possible. Zopf, on the other hand, distinctly denies the occurrence of any appearance of fusion. The membrane of the sac-cells generally consists of cellulose; in some cases (species of *Fumaria* and *Corydalis*) the wall becomes lignified and thickened, and is then provided with obliquely placed pits. The opinions of authors differ as to the contents of the sac-cells.

Léger in his works, especially the last and most extensive, classes the sac-cells in question with the laticiferous sacs and articulated laticiferous tubes of the Papaveraceae, and in this, at any rate, he goes too far; he unreservedly describes the contents as latex. On the basis of an investigation of *Hypecoum, Corydalis, Adlumia, Dicentra* and *Fumaria*, the same author states that this latex is always clear and usually red or yellow, rarely colourless, and that in the genera *Hypecoum, Adlumia, Dicentra* and *Fumaria*, the latex disappears completely or in part in the fully grown aerial organs. Zopf, who originally and, as Heinricher has shown, quite incorrectly described the sac-cells as tannin- and anthocyanin-receptacles, confounding them with true anthocyanin-receptacles, now defines the sac-cells as alkaloid-receptacles, on the ground of quantitative and qualitative analyses, which were carried out on the subterranean organs of *Corydalis*. This needs further confirmation at any rate with regard to the remaining members of the Order. It has been already stated above that Heinricher adheres, and it is probably best to do so, to the name sac-cells; he also states that the contents are a mixture of different substances, but always include a fatty oil.

In connexion with the sac-cells it may also be mentioned that, according to Léger, 'petits canaux laticifères' filled with similar contents occur in the primary cortical parenchyma; these are probably nothing more than small intercellular spaces, filled with secretion, such as have been observed elsewhere in plants with secretory organs which produce latex.

The following anatomical features of the Order remain to be mentioned. The **branches** contain a ring of vascular bundles, according to Léger the interfascicular tissue of the latter is lignified. The pericycle is generally sclerenchymatous; *Corydalis solida*, Sm., forms an exception to this. According to Léger, the **mesophyll** is mostly bifacial; *Hypecoum procumbens*, L., has palisade-tissue on both sides of the leaf. **Stomata** occur on both surfaces of the leaf, or on the lower side only; they possess no characteristic subsidiary cells. It is especially noteworthy, that the pair of guard-cells does not always show a round outline, but sometimes (*Dicentra spectabilis*, Lem., *D. formosa*, Walp., *Adlumia cirrhosa*, Raf., *Corydalis claviculata*, DC., *Fumaria capreolata*, L.) a polygonal one, in which the corners are

often produced into filiform tips. **Oxalate of lime** appears to be absent. Special forms of hairs and glandular hairs have not been observed. The petiole, which has been examined by Petit in species of *Adlumia, Corydalis, Fumaria*, and *Hypecoum*, possesses in its characteristic region ('caractéristique') an arc of three or more isolated vascular bundles, in the initial region it usually has three (in *Dicentra* nine). According to Plitt, the vascular bundles of the petiole are characterized by the concave excavation of the xylem-group on its outer side, as in the Ranunculaceae.

The fibro-vascular system of the root is diarch, according to De Bary, Zopf, Léger and others; the peculiar splitting of the older roots and rhizomes of the Fumariaceae is worthy of note (for this see Jost, Bot. Zeitung, 1890, p. 469 et seq.).

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CRUCIFERAE.

1. Review of the Anatomical Features. The Cruciferae are a well characterized Order, both in their external features and in respect to their anatomy. All the Cruciferae possess characteristic secretory cells; their essential constituent is myrosin, which is widely distributed in the Order. These elements may consequently be termed myrosin-cells. The type of stoma, known under the name Cruciferous type, is almost constant, although sometimes obliterated in the fully formed organs; the pair of guard-cells is surrounded by three subsidiary cells, of which one is smaller than the two others. The perforations of the vessels are simple. The wood-prosenchyma has simple pits. Where cork occurs, it originates in the pericycle or in the inner part of the primary cortex. Medullary-ray-parenchyma is usually absent in the xylem: the primary medullary rays of the wood are only rarely (*Raphanus, Rapistrum*) parenchymatous, and are mostly replaced by interfascicular prosenchyma; secondary medullary rays consisting of parenchyma are also uncommon. Crystals of oxalate of lime have not been observed in the vegetative organs. Clothing hairs are in all cases unicellular, but at the same time have various shapes, viz. simple unbranched hairs (Fig. 15, *A*), forked Y-shaped hairs (Fig. 15, *B*), two-armed hairs (Fig. 15, *C*), stellate hairs (Fig. 15, *D–E*), peltate hairs (Fig. 15, *F*), and dendroid hairs (Fig. 15, *G*); their walls are sometimes incrusted with carbonate of lime. Glandular hairs (Fig. 15, *B*) or glandular emergences (Fig. 15, *H–J*) are rare (*Hesperis, Bunias, Matthiola*, and allied genera). Besides the different forms of trichomes just named, the following additional features can be employed especially for the diagnosis of genera and species: (*a*) the extremely remarkable differentiation of the integumental tissue of leaf and stem (Fig. 14), which is present in many Cruciferae, and is due to the occurrence of single large water-storing cells, or of rows of these, among the ordinary epidermal cells which surround the stomata; (*b*) the distribution of myrosin-cells in different tissues and organs; (*c*) the varied differentiation of the ring of vascular bundles in the stem; (*d*) the varied nature of the xylem in the root, &c.

Lastly, the following noteworthy structural features of the stem and root respectively of certain members of the Order may be briefly indicated: the occurrence (*a*), in the wood of *Vella spinosa*, Boiss. (Fig. 16) and also of *Brassica fruticulosa*, of concentric zones consisting of unlignified xylem-tissue with spirally thickened tracheae inclosed in it; (*b*) of medullary vascular bundles (rhizome of *Cochlearia Armoracia* and tuberously thickened parts of the stem of Kohlrabi); (*c*) of cortical vascular bundles (*Eruca sativa* and *Lepidium latifolium*); (*d*) lastly, of interxylary concentrically constructed vascular bundles (rhizome of *Cochlearia Armoracia*, root of *Brassica Rapa*, *B. Napus* and *Raphanus sativus*).

2. Structure of the Leaf. The **mesophyll** possesses varied structure; centric leaf-structure is found, for example, in *Matthiola livida*, DC., *Anastatica hierochuntica*, L., *Moricandia arvensis*, *Crambe maritima*, &c. The lateral walls of the **epidermal cells** are usually undulated to a varying extent. Bead-like thickenings of the cuticle are described in *Diplotaxis tenuifolia*; striation of the cuticle occurs, for example, in *Lepidium subulatum*, *Iberis sempervirens*, &c. Further, excretion of wax also occurs on the leaves, in considerable amount,

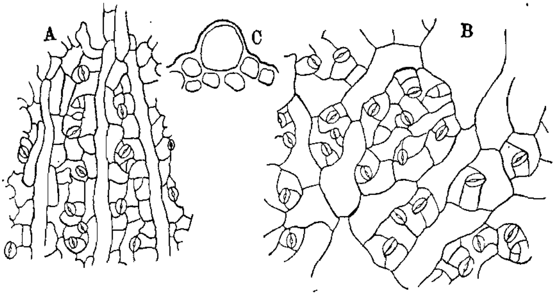

Fig. 14. Differentiation of the epidermis in the Cruciferae. Epidermis of the leaf of: A, *Heliophila amplexicaulis*; B, *Moricandia arvensis*; C, *Eruca cappadocica*. A and B, in surface-view; C, in cross-section.—After Heinricher.

for example, in *Brassica oleracea*. Gelatinization of the inner membranes of the epidermal cells has so far only been determined (Warming) in *Cakile aequalis*, L'Hérit. **Stomata** are usually met with on both sides of the leaf, rarely (*Lunaria rediviva*) only on the lower side. They are generally of the well-known Cruciferous type, i.e. they are surrounded by three subsidiary cells, of which one is smaller than the other two. For the mother-cell of the stoma in the Cruciferae divides by three or four successive division-walls, which follow one another like the segments of a three-sided apical cell. However, exceptions to this type occasionally occur (*Subularia*, according to Benecke). The vascular bundles of the **veins** are embedded in the mesophyll, or are united with the upper and lower epidermis by means of colourless parenchyma; sclerenchyma accompanying the vascular bundles is wanting, both here and in the petioles, which will be discussed later.

An extremely characteristic differentiation of the epidermis of the leaf (Fig. 14, *A–C*), which Heinricher has investigated in detail, is frequently found in the Order, but is restricted to certain species only. This differentiation con-

sists in the fact that among the ordinary epidermal cells others are intercalated, which exceed the remaining cells many times (10 to 20 to even 100 times) in volume, and at the same time project considerably beyond the level of the other epidermal cells, sometimes almost like hairs in a transverse section of the leaf. The contents of these cells do not differ from those of the adjacent ordinary epidermal cells; i.e. they are colourless, like those of the latter. The function of these special cells of the epidermis is the storage of water.

In the first place, in *Goldbachia torulosa*, DC., there are only isolated epidermal cells, which exceed the others three or four times in size. Isolated large epidermal cells occur also in *Isatis tinctoria*, L., *Senebiera Coronopus* and species of *Heliophila*; in these species, however, small groups of the large cells are found as well. A still further degree of differentiation is attained when the large cells, which are sometimes (*Diplotaxis acris*) provided with small knobs on their outer walls, are arranged in series; they then form a network on the surface of the leaf, which may often be recognized even with the naked eye, and the meshes of which are occupied by island-like groups of stomata with the subsidiary cells belonging to them. According to Heinricher this is the case in *Raphanus sativus*, and is still more pronounced in *Eruca cappadocica* (Fig. 14, *C*), *Diplotaxis tenuifolia*, DC., and *Moricandia arvensis* (Fig. 14, *B*); according to Volkens also in *Malcolmia aegyptiaca*, Spreng., *Diplotaxis acris*, Boiss., and *Savignya parviflora*, Webb. While in the species so far enumerated the large epidermal cells in question have no specially marked long axis in surface-view, but are of fairly equal diameter in all directions in the leaf-surface, in some species of *Heliophila*, e.g. *H. amplexicaulis* (Fig. 14, *A*) or *H. pilosa*, they form elongated sacs, which may sometimes attain a length of 8 mm.

This differentiation of the epidermis occurs also in the stem, as was first shown in *Senebiera* and *Hutchinsia* by Dennert, and afterwards in a series of species by Volkens and Heinricher.

The **secretory cells**, which are quite generally distributed in the Order, deserve special notice. They were termed proteid-sacs by their discoverer, Heinricher, on account of the proteid reactions of their contents, but, according to Guignard and Spatzier, they are the seat of the myrosin; they are therefore spoken of as myrosin-cells in the following description. It is well known that myrosin is a very widely distributed ferment in the Cruciferae; by its action on a glucoside (likewise occurring in the Order), viz. myronate of potash, a decomposition of the latter takes place with formation of mustard-oil, sugar and bisulphate of potash. The first of these substances, the mustard-oil, gives the characteristic slight radish-like or strong mustard-like pungency to all parts of the plant—the seed, root, stem, leaf, &c. The myrosin-cells are specially easily recognizable by the reactions of their contents. In their natural unaltered condition it is sometimes difficult to recognize them, for often they scarcely differ morphologically from the neighbouring cells; only in the cortex and in the mesophyll are they distinguished from the adjacent cells by their greater length; in the leaf they sometimes stand out as branched shortly 3–4-armed idioblasts; in the pericycle of the vascular bundles of the veins they occasionally form rows. In living material the myrosin-cells are primarily distinguished by the constant absence of chlorophyll-grains and usually[1] also of starch-grains, and by their clear, aqueous, optically inactive contents. Detection of the myrosin-cells is further facilitated by the different reactions for myrosin, which are specified in tabular form in Spatzier's work. Of these I will only mention Millon's reagent, by which the contents are coagulated and coloured red, the golden yellow coloration of the contents by watery solution of iodine, the coagulation of the myrosin by alcohol, the staining by aniline dyes, the violet coloration caused by concentrated hydrochloric acid with the addition of orcin- or orcein-solution; plasmolysis also renders the myrosin-cells apparent. The behaviour

[1] Perennial organs, such as the rhizome of *Cochlearia Armoracia*, the cells of which are filled with large starch-grains, also store up small-grained starch in the myrosin-cells (Spatzier).

towards myronate of potash, which affords an important means of demonstrating the myrosin contained in the cells in question, is not of further use for the detection of the myrosin-cells themselves. As regards the distribution of these cells one may safely say, on the basis of the statements of Heinricher and Guignard, that they are quite generally[1] distributed in the Cruciferae, although still more abundant material must be investigated with regard to this point. The exceptional cases (*Capsella bursapastoris*, Moench., *Lepidium sativum*, L., *Camelina sativa*, Crantz, *Bunias orientalis*, L., *Cakile maritima*, Scop.), in which Heinricher was unable to find his proteid-sacs, have been disposed of by Guignard, for he demonstrated myrosin-cells in these also. It should, however, be remarked that the amount of myrosin-cells may vary in the same species. Thus it has been proved by means of experimental researches by Spatzier and by corresponding observations by Guignard, that habitat and nutrition exert an influence on the abundance of the myrosin-cells. It may be added, however, that this never leads to a complete suppression of their formation, and further that an increase in myrosin-formation sets in when the development of the plant is checked. The myrosin-cells are found in all the organs of the plant, e.g. root, branch, leaf, flower, and seed. They are often present in greatest abundance in the root; sometimes they are extremely scanty in the vegetative organs, but are then fairly easy to find in the seed or in the ovary.

With regard to the topographical distribution of the myrosin-cells in the different vegetative organs it is necessary to make the following statements. The roots contain myrosin-cells in the primary cortex and in the bast; tuberous roots (*Raphanus sativus*, *Cochlearia Armoracia*) contain them in the wood-parenchyma as well. Guignard mentions the following cases, in which he has found the myrosin-cells to be fairly abundant in the phloem-parenchyma of the roots: *Cheiranthus Cheiri*, L., *Barbarea vulgaris*, R. Br., *Nasturtium amphibium*, R. Br., *N. sylvestre*, R. Br., *Lunaria biennis*, Moench, *L. rediviva*, L., *Cochlearia officinalis*, L., *Brassica oleracea*, L. with varieties, *B. nigra*, Koch, *Sinapis alba*, L., *S. arvensis*, L., *Lepidium Draba*, L., *L. latifolium*, L., *Iberis amara*, L., *I. semperflorens*, L., *I. umbellata*, L., *Cakile maritima*, Scop. Guignard recommends the radish as specially suitable for the study of the myrosin-cells of the root.

In the branch the myrosin-cells may appear in all the tissues; they are specially common in the pericycle, where moreover they always occur. With regard to their more precise distribution the following examples of Guignard's may be quoted. The myrosin-cells are found:

(1) exclusively in the pericycle in: *Lepidium sativum*, L., *L. Draba*, L., *L. Iberis*, Pollich, *Camelina sativa*, Crantz, *Cardamine pratensis*, L., *Cheiranthus Cheiri*, L.;

(2) principally in the pericycle, but also in the primary and secondary bast in: *Erysimum cheiranthoides*, L.;

(3) principally in the primary cortex[2], but also in the pericycle: *Moricandia hesperidifolia*, DC.;

(4) in the primary cortex, in the primary and secondary bast, and in the pericycle in: *Iberis semperflorens*, L., *I. amara*, L., *I. umbellata*, L.;

(5) in the primary cortex, in the pericycle, and in the pith in: *Nasturtium officinale*, R. Br., *Eruca sativa*, Lam.;

(6) in the primary cortex, in the pericycle, and in the secondary bast in: *Bunias orientalis*, L., *B. Erucago*, L., *Nasturtium sylvestre*, R. Br.;

(7) in the primary cortex, pericycle, secondary bast and pith in: *Nasturtium amphibium*, R.Br., *Diplotaxis tenuifolia*, DC., *Raphanus sativus*, L., *Isatis tinctoria*, L.;

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[1] Myrosin-cells have been demonstrated by Heinricher, Volkens and Guignard in species of the following genera: *Aethionema*, *Arabis*, *Barbarea*, *Brassica*, *Bunias*, *Cakile*, *Camelina*, *Capsella*, *Cardamine*, *Carrichtera*, *Cheiranthus*, *Cochlearia*, *Corispora*, *Crambe*, *Diplotaxis*, *Eruca*, *Erucastrum*, *Erysimum*, *Farsetia*, *Goldbachia*, *Heliophila*, *Hesperis*, *Iberis*, *Ionopsidium*, *Isatis*, *Lepidium*, *Lunaria*, *Malcolmia*, *Moricandia*, *Myagrum*, *Nasturtium*, *Peltaria*, *Raphanus*, *Rapistrum*, *Senebiera*, *Sinapis*, *Sisymbrium*, *Succovia*, *Teesdalia*, *Vella*, *Zilla*.

[2] I believe this to be the correct interpretation of the tissue simply termed 'écorce' by Guignard.

(8) principally in the primary cortex and pericycle, but also in the primary and secondary bast and in the pith in: *Brassica nigra*, Koch, *Sinapis alba*, L., *S. arvensis*, L.;

(9) in the primary cortex, pericycle, primary and secondary bast, the wood-parenchyma and pith in: *Cochlearia Armoracia*, L., and *C. officinalis*, L.

In the leaf the myrosin-cells are in general present in greater abundance than in the axis. They mostly appear in the leaf as distinct idioblasts on account of their length. They are principally found in the spongy tissue, but also in the palisade-tissue; they also occur in the parenchymatous sheaths surrounding the vascular bundles of the veins and in the bast and pericycle of these bundles. The diverse distribution of the elements in question is seen in the following table taken from Heinricher's work. The myrosin-cells

(1) are distributed in the mesophyll of the leaf in: *Arabis sagittata, Cochlearia Armoracia, Peltaria alliacea, Chorispora tenella, Camelina austriaca, Isatis tinctoria, Myagrum perfoliatum, Brassica* sp., *Sinapis alba, Diplotaxis tenuifolia, Erucastrum arabicum, Eruca cappadocica, Carrichtera Vella, Vella Pseudocytisus, Crambe cardifolia, Rapistrum perenne, Raphanus sativus* and *Heliophila amplexicaulis*;

(2) are only in part scattered in the mesophyll; they mostly represent single cells of the parenchymatous sheaths of the vascular bundles in the veins or they abut directly on the bundles of the veins: *Iberis sempervirens, I. semperflorens* and *Goldbachia torulosa*; probably also *Lepidium Draba*, L., and *L. sativum*, L., according to Guignard;

(3) are only found in place of single cells of the parenchymatous sheaths of the veins: *Cheiranthus Cheiri, Lepidium affine, Senebiera Coronopus*;

(4) are only found accompanying the vascular bundles of the veins on the inner side of the parenchyma-sheath (in the pericycle and bast): *Hesperis matronalis*; also, according to Guignard, *Iberis amara*, L., *I. umbellata*, L.;

(5) occur in the mesophyll in a sub-epidermal position only: *Moricandia arvensis*, which in the axis also, according to Heinricher, possesses myrosin-cells in a sub-epidermal position only.

From the above synopsis of the distribution of the myrosin-cells in the axis and leaf it follows that in some cases the mode of distribution certainly enables one to recognize affinities, but that in general it will only be of sufficient value for specific diagnosis.

Following on the description of the myrosin-cells some mention must also be made of Dutailly's statement as to the occurrence of schizogenous secretory passages in the root of certain Cruciferae and the subsequent differentiation of a concentric vascular bundle around these secretory organs. This statement, however, is erroneous according to J. E. Weiss.

As has already been mentioned under the general characters, crystals of **oxalate of lime** have not been observed so far in the vegetative organs of the Cruciferae. On the other hand, sphere-crystals, which appear to be closely related to hesperidin, are stated by Mika, Hansen, and Schaarschmidt to occur in *Capsella Bursa-pastoris*.

Apart from the external glands to be discussed below, the **hairy covering** consists of clothing hairs of various forms, which are, however, always unicellular. It is true that (e.g. in *Capsella*, Fig. 15, *A*, or sometimes in *Arabis alpina*) near the base of the hair an annular line may be observed, which appears like a division wall, but according to Vesque is not a septum. The wall of the hairs may be thin or thick, smooth or furnished with knobs. The thick walls of the hairs and the knobs are sometimes (e.g. in *Alyssum alpestre* and *Cheiranthus Cheiri*) incrusted with carbonate of lime. The form of the hairs is very varied; thus the following types occur: simple unbranched hairs, simple forked hairs, two-armed hairs, few- or many-rayed stellate hairs, scales and dendroid hairs. The diverse forms of hairs may without doubt be employed systematically for specific diagnosis, though with some caution. For in the same species two or more forms of hairs are sometimes found, and, moreover, these are connected by numerous transitional forms.

Vesque describes simple hairs in *Lepidium, Isatis, Sinapis, Capsella* (Fig. 15, *A*), *Eruca, Diplotaxis, Raphanus,* &c. Simple forked hairs (i.e. hairs which are only once acutely forked) are found side by side with simple hairs in *Draba aizoides, D. hispanica,* Boiss., and also in *Draba verna,* forked hairs only in *Bunias orientalis*

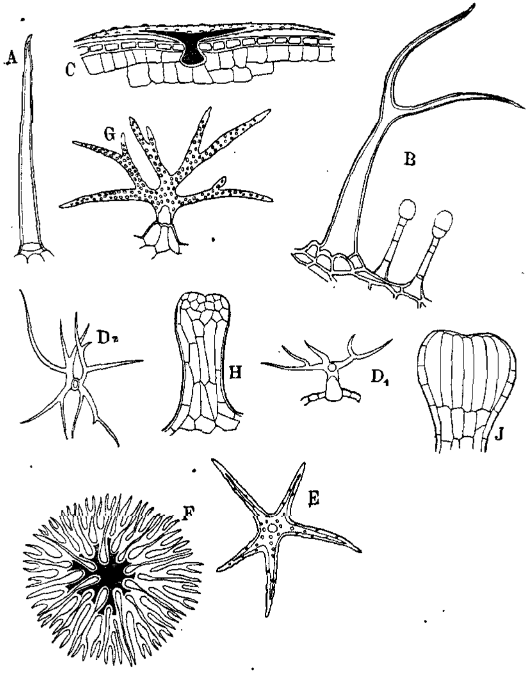

FIG. 15. Trichomes of the Cruciferae. A, Simple hair from the upper side of the leaf of *Capsella Bursa-pastoris.* B, Forked hair and glandular hair of *Hesperis glutinosa,* Vis., from the floral region. C, Two-armed calcified hair from the leaf of *Cheiranthus Cheiri,* L. D_1 and D_2, Stellate hair, from the leaf of *Matthiola livida,* DC., in surface-view and from the side. E, Stellate hair from the lower side of the leaf of *Capsella Bursa-pastoris.* F, Peltate hair of *Alyssum lepidotum,* Boiss. G, Dendroid hair from the lower side of the leaf of *Alyssum saxatile.* H and J, External glands of *Matthiola livida*: H, Entire glandular hair seen from the side; J, Longitudinal section through the glandular head.—A, E and G, after Vesque; F, after O. Bachmann; the remainder original.

and *Hesperis glutinosa,* Vis. (Fig. 15, *B*); two-armed (so-called malpighian) hairs have been observed in *Cheiranthus alpinus* and *C. Cheiri* (Fig. 15, *C*), in *Erysimum canescens, Farsetia aegyptia,* Turra, and also in *Capsella* and *Erysimum cheiranthioides,* in the last two accompanying other forms of hairs. To the type of stellate hairs (by which are to be understood those branched hairs, in which the

rays lie in the same place, the latter being parallel to the surface of the organ) belong the hairs of *Capsella Bursa-pastoris* (Fig. 15, *E*), *Erysimum aureum*, *Alyssum alpestre*, *A. petraeum*, *Matthiola incana*, *M. livida*, DC. (Fig. 15, D_1–D_2), *Malcolmia aegyptiaca*, Spreng. The elegantly constructed stellate hairs of *Alyssum lepidotum*, Boiss. (Fig. 15, *F*), which resemble small scales, must be referred to the preceding type. Lastly, the dendroid hairs remain to be mentioned; in these a stem-like part arises immediately from the broadened basal part, and after a short distance divides into 2–4 diverging branches, which in their turn may be repeatedly forked—sometimes, e.g. in *Matthiola arborescens*, with unequal growth of the successive dichotomous branches after the manner of a scorpioid cyme. One meets with this category of hairs, e.g. in *Farsetia incana*, *Matthiola arborescens*, *Alyssum petraeum*, *A. saxatile* (Fig. 15, *G*), and *Draba* sp.[1]

Glandular hairs or external glands of more complicated structure are of rare occurrence in the Order, and, according to Prantl, characterize the 'Hesperideae-Hesperidinae[2].' In *Hesperis* they consist of a row of cells with one or few glandular terminal cells (Fig. 15, *B*). The glandular structures of *Bunias*, on the other hand, form short emergences resembling shaggy hairs, the apex being occupied by a group of cells, which are filled with a secretion and have a palisade-like shape. The glandular shaggy hairs of *Matthiola livida*, DC. (Fig. 15, *H–J*), are similarly constituted.

The glandular leaf-teeth, investigated by Reinke in *Lepidium latifolium* and *Alliaria officinalis*, may also be shortly mentioned here. In the first of these plants the leaf-tooth contains a hyaline group of cells covered by an epidermis composed of peculiarly striated cells and containing a group of stomata; in the second plant the leaf-tooth incloses a mucilage-containing group of cells (in which a branch of a vein terminates) and possesses an epidermis with numerous stomata.

The **petiole** has been investigated by Vesque, Plitt, and Petit in a number of Cruciferae. It may first be noted that the vascular bundles in the characteristic region are isolated, as in the majority of herbaceous plants. They form either a ring or a horseshoe; medullary bundles are rare (in the stout petioles of *Crambe cordifolia* and *Cochlearia Armoracia*); the number of the bundles forming the ring or horseshoe respectively varies, there is usually a rather large number, rarely (*Cochlearia officinalis*) only three or even only one (*Teesdalia nudicaulis*). In certain members of the Order some of the vascular bundles, which form the ring or the horseshoe, are not simple but compound; they then consist of several vascular bundles arranged in a circle. Such compound bundles have been stated by Plitt and Petit to occur in species of *Brassica*, *Cochlearia* (*C. Armoracia*), *Crambe*, *Lunaria*, *Nasturtium*, *Raphanus*, *Rapistrum*, and *Sinapis*, but were not found by these authors in species of *Alyssum*, *Barbarea*, *Capsella*, *Cardamine*, *Cheiranthus*, *Cochlearia* (*C. officinalis*), *Erysimum*, *Farsetia*, *Hesperis*, *Iberis*, *Lepidium*, *Sisymbrium*, *Syrenia*, and *Teesdalia*.

3. STRUCTURE OF THE AXIS. The inner walls of the **epidermis** are usually strongly thickened. Sclerotic differentiation of the epidermis has been observed in *Arabis procurrens*, doubling of the epidermis in *Diplotaxis Harra*, Boiss., and *Zilla myagroides*, Forsk.

The **primary cortex** is frequently collenchymatous in its outer portion, the collenchyma either forming a ring or only strands. Spaces are found in the primary cortex in plants which live in damp localities, e.g. *Nasturtium officinale*, *Cardamine pratensis*. In some desert-plants (*Malcolmia aegyptiaca*, Spreng., and *Zilla myagroides*, Forsk.) the assimilatory tissue of the primary cortex is formed by palisade-tissue. In *Oudneya africana*, R. Br., another

[1] Compare also Dennert's statements as to the hairy covering of the axis, in Wigand, Bot. Hefte i, 1885, p. 101; the statements, however, only refer to the bare form of the hairs.

[2] In this tribe Prantl classes the genera: *Hesperis*, *Matthiola*, *Lonchophora*, *Pyramidium*, *Bunias*, *Zerdana*, *Sterigma*, *Anchonium*, *Dontostemon*, *Chorispora*, *Christolea*, *Parrya*, and *Clausia*.

desert-plant investigated by Volkens, the primary cortical tissue possesses quite a peculiar structure ; its outermost 5–6 layers consist of cells, which have rounded lumina and are elongated in the vertical direction, their walls being unlignified, but spirally to reticulately thickened ; these cells clearly serve as a water-reservoir. The innermost layer of cells of the primary cortex is frequently (*Brassica, Capsella, Kernera, Lepidium, Nasturtium, Sinapis,* &c.) differentiated as a starch-sheath.

In shrubby species periderm-formation takes place either in the innermost layers of the primary cortex or (*Arabis procurrens* and *Aubrietia deltoidea*) between primary hard and soft bast.

With regard to the structure of the **pith** it is only necessary to mention that in the older branches of *Diplotaxis Harra,* Boiss. this tissue becomes septate (Volkens), and that sometimes (*Zilla myagroides,* Forsk.) the peripheral part of the pith is composed of a prosenchymatous sheath of sclerenchyma.

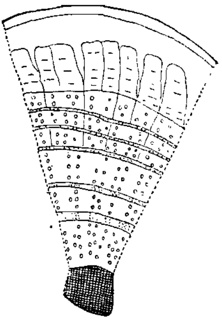

FIG. 16. Piece of a transverse section of a branch of *Vella spinosa*, Boiss., diagrammatic. (The small-lumened spiral vessels in the narrow *concentric zones are indicated by dots; in the* bast the groups of bast fibres are represented by lines: see text.)—Original.

The following statements may be made regarding the ring of **vascular bundles** and the elements composing it. The xylem is principally formed of vessels, which have lumina of various sizes and are provided with simple perforations, and of wood-prosenchyma with simple pits. Parenchymatous medullary rays are absent in most Cruciferae. Primary parenchymatons medullary rays have only been met with in species of *Raphanus* and *Rapistrum,* while secondary medullary rays are somewhat more frequently developed (in *Cheiranthus, Matthiola, Peltaria, Isatis,* &c.). In most members of the Order the primary medullary rays are replaced by prosenchymatous (interfascicular) tissue. Intraxylary phloem is not present in the Cruciferae. The tissue which Dennert, with the necessary reserve, and Plitt as well as Borzi, definitely, regarded as internal soft bast, is merely protoxylem (Briquet). With regard to the external phloem it need only be stated that it is generally accompanied by strongly developed primary hard bast, and that secondary hard bast has been observed in woody species. On the subject of the detailed structure of the hard bast and of the ring of vascular bundles, a tabular review in Dennert's work quoted above gives more exact information. This can only be shortly referred to, as the types of stem-structure set up by Dennert are only of importance for specific diagnosis, and do not correspond to definite systematic groups of genera.

A transverse section of the mass of wood in *Vella spinosa,* Boiss. (Fig. 16) shows a special type of differentiation. It is traversed by narrow concentric zones of unlignified cellular tissue, containing small-lumened vessels, which differ from the spirally thickened pitted vessels present elsewhere in this species, in having exclusively spiral or reticulate thickening of their walls. A structure similar to that of *Vella* also occurs in *Brassica fruticulosa,* Cyr., judging by Borzi's treatise, but has been quite erroneously interpreted by Borzi as an occurrence of interxylary phloem.

Cortical vascular bundles have been observed by Dennert in *Eruca sativa* and *Lepidium latifolium.* Further, according to J. E. Weiss and Dutailly, medullary and interxylary vascular bundles, both of concentric structure, are

present in some Cruciferae. The former, the medullary bundles, are found in the pith of the rhizome of *Cochlearia Armoracia*, as well as in the tuberously thickened parts of the stem of kohlrabi. The latter, the interxylary bundles, arise secondarily in the unlignified xylem of the rhizome of *Cochlearia Armoracia*, and, it may be added, also in the xylem of the root of *Brassica Napus*, *B. Rapa*, and *Raphanus sativus*; they are downward prolongations of parts of the vascular bundle-system, belonging to the aerial part of the plant.

4. Structure of the **root**. The vascular system of the root in the Cruciferae is usually diarch in development. For further detail as to the structure of the root in general, see Lohrer's work cited below.

The occurrence of characteristic thickening-ridges, exhibited by the layer of cells immediately outside the endodermis in the roots of many members of the Order ('réseau de soutien' = 'réseau sus-endodermique' of Van Tieghem) specially deserves mention. Russow was the first to meet with this anatomical feature in the root of the cabbage, and Van Tieghem has demonstrated it in the following genera: *Matthiola, Cheiranthus, Arabis, Alyssum, Koniga, Farsetia, Berteroa, Vesicaria, Clypeola, Draba, Cochlearia, Thlaspi, Iberis, Biscutella, Malcolmia, Sisymbrium, Alliaria, Hugueninia, Syrenia, Camelina, Lepidium, Isatis, Sinapis, Hirschfeldia, Brassica, Eruca, Erucastrum, Succovia, Crambe, Rapistrum, Enarthrocarpus, Erucaria, Raphanistrum, Raphanus, Heliophila, Schizopetalum* and *Leptocarpaea.*

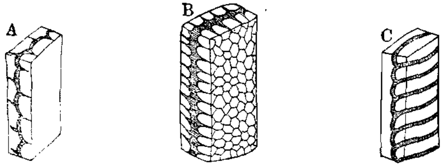

FIG. 17. Diagrammatic representation of the cells of the epi-endodermal network ('réseau sus-endodermique') to show the manner of thickening of their walls: A, *Iberis affinis*; B, *Sinapis alba*; C, *Lepidium sativum*.—After Van Tieghem.

According to Van Tieghem this layer of cells provided with thickening-ridges is not developed in the genera: *Nasturtium, Roripa, Barbarea, Turritis, Notoceras, Tetrapoma, Teesdalia, Ochthodium, Chorispora, Hesperis, Erysimum, Ionopsidium, Myagrum, Goldbachia, Diplotaxis, Bunias,* and *Senebiera.* It should be remarked in connexion with the first list of genera having a 'réseau de soutien,' that differences occur within the genus as to the earlier or later appearance of the thickening-ridges and as to the distribution of the latter in all or only in some of the cells of the layer concerned (external to the endodermis). The feature in question is sometimes wanting in one or other species of the genera named (e.g. in *Eruca cappadocica*). The manner of thickening of the cells is different in different species. In all the species thickening-ridges, which are either straight (*Sinapis alba*) or composed of smaller arcs with their convexities directed outwards (*Cheiranthus Cheiri*, &c.), occur in the middle line of the radial and horizontal walls of the cells concerned. In each cell these thickening-ridges together form a rectangle; they correspond in adjacent cells, and consequently they collectively form a network, having rectangular meshes and developed in the tangential direction. Further thickening-ridges on the radial and horizontal walls are attached at right angles to these principal ridges; some of them run towards the outer, some towards the inner tangential wall of the cell; the former never extend on to the outer tangential wall of the cell, which is always free from secondary thickening; the latter behave similarly (*Iberis affinis*, Fig. 17, *A*), or they form either a network (*Sinapis alba*, Fig. 17, *B*, *Cheiranthus Cheiri*, *Alyssum minimum*) or a parallel system of striae (*Lepidium sativum*, Fig. 17, *C*, *Schizopetalum Walkeri*) on the inner tangential wall of the cell.

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CAPPARIDEAE.

1. Review of the Anatomical Features. Uniform structural features, which characterize the whole Order, are only present in small number. Foremost among these are the following characters: the vessels of the wood have simple perforations; the wood-prosenchyma bears simple pits; the stomata in the mature leaf are surrounded by several epidermal cells, which are not differentiated by their shape; oxalate of lime very rarely appears in the form of ordinary large solitary crystals, and is usually only present in the form of clustered crystals or small prismatic crystals. The presence of special secretory cells, viz. myrosin-cells, which have so far only been observed in the genera *Capparis*, *Cleome*, *Gynandropsis*, and *Polanisia*, but are probably more widely distributed in the Order, and the occurrence of two-armed and of branched unicellular hairs (Fig. 19, *B–C*) in certain species of *Capparis* thus suggest, on anatomical grounds, the relationship of the Capparideae to the Cruciferae. Apart from the above features, great diversity of anatomical structure prevails within the Order. The numerous anatomical characters can moreover only be employed to a small extent in generic diagnosis, and are usually solely of value in specific diagnosis; some of them are suitable for the recognition of certain species as members of their Order. Examples of the former characters (those

chiefly distinguishing species) are: the different types of leaf-structure and the varied differentiation of the mesophyll; fissures in the mesophyll which are due to drying and cause small transparent striae in the leaf (species of *Capparis*, *Forchhammeria*, and *Morisonia*); sclerenchymatous elements of varied structure in the mesophyll (Fig. 18, *B–C*), either approximately isodiametric and scarcely branched or unbranched (species of *Capparis*, *Cadaba*, and *Niebuhria*), or branched on all sides (species of *Capparis*, *Niebuhria*, and *Thylachium*), or elongated like palisade-tissue and with branched or unbranched ends (species of *Boscia*, *Capparis*, *Courbonia*, *Niebuhria*), or fibrous and running irregularly in the mesophyll (species of *Boscia*, *Cadaba*, and *Capparis*); the varied marking of the cuticle; the papillose differentiation of epidermal cells on the lower side of the leaf (species of *Courbonia*, *Crataeva*, *Isomeris*, and *Wislizenia*); the development of a hypoderm on the upper side of the leaf

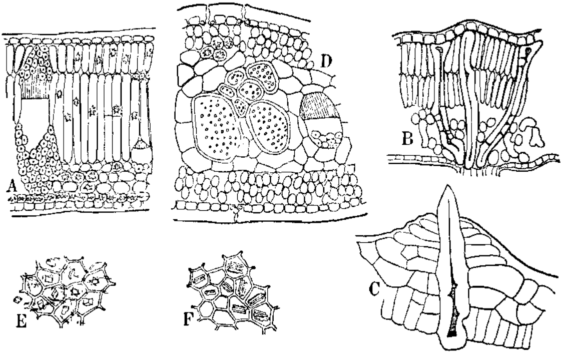

FIG. 18. A Transverse section through the leaf of *Capparis zeylanica*, L. B, Transverse section through the leaf of *Capparis odoratissima*, Jacq., with fibrously elongated spicular cells converging towards the base of a hair. C, Hair like spicular cell of the leaf of *Capparis domingensis*, Spreng. D, Transverse section of the leaf of *Capparis galeata*, Fres., with reservoir-tracheides. E, Upper epidermis of the leaf of *Capparis Cynophallophora*, L., with crystals of gypsum. F, Upper epidermis of the leaf of *Capparis polyantha*, Tr. et Pl., likewise containing crystals of gypsum.—C, *Original*; *the remainder after Vesque.*

(species of *Capparis*); the structure of the veins of the leaf, of the midrib, and of the petiole; lastly, the different forms of clothing hairs (Fig. 19), namely simple unicellular hairs, unicellular two-armed hairs (species of *Capparis*), unicellular stellate hairs (species of *Capparis*), simple uniseriate trichomes, emergences resembling shaggy hairs (species of *Cadaba*, *Capparis*, and *Morisonia*), multicellular hairs of various shapes (species of *Capparis* and *Steriphoma*), candelabra-hairs (species of *Capparis*), and lastly, peltate hairs with varied structure (species of *Atamisquea*, *Cadaba*, *Capparis*, and *Morisonia*). Among the characters, by which certain Capparideae can at once be recognized as members of their Order, the following should be especially enumerated: (*a*) the occurrence of peltate hairs with a small 'upper scale' (Fig. 19, *M*) in *Atamisquea*, in species of *Capparis* and in *Morisonia*; (*b*) the occurrence of gypsum (Fig. 18, *E–F*) in the form of small prismatic crystals or of sphaerocrystalline masses in species of *Capparis*, *Cladostemon*, and *Thylachium*. To what

has been said above regarding the secretory organs of the Capparideae, it should be added that mucilaginous epidermal cells have not been observed in any case, further that in the Cleomeae peculiar secretory cells, requiring more detailed investigation, occur in the immediate neighbourhood of the vascular bundles of the veins, that Vesque found mucilage-cells in the mesophyll and in the parenchyma of the veins of the leaf in some Cappareae, and lastly, that external glands of varied structure are scantily represented in the Cappareae, more abundantly in the Cleomeae. Finally, anomalous stem-structure in the form of 'renewed successive rings of growth' has been shown to occur in the genera *Maerua*, *Roydsia*, *Cadaba*, and *Forchhammeria*; the secondary rings of bundles are either intrafascicular or extrafascicular in origin.

2. Structure of the Leaf. The **leaf-structure** is well known, owing to the researches of Vesque, Radlkofer and Blenk. The structure of the leaf belongs either to the centric or to the bifacial type. The former occurs in species of *Maerua* (e.g. *M. senegalensis*, R. Br.), in *Courbonia glauca*, Brongn., in most species of *Cadaba*, in species of *Boscia* (e.g. *B. microphylla*, Oliv.), in many species of *Capparis*, and also in the Cleomeae (e.g. *Cleome chrysantha*). Bifacial leaf-structure has been observed in species of *Thylachium*, *Steriphoma*, *Morisonia*, *Niebuhria*, *Maerua* (e.g. *M. angustifolia*, Rich.), in *Cadaba trifoliata*, W. et A., in species of *Boscia* (e.g. *B. urens*, Welw.), in many species of *Capparis* (e.g. *C. Nummularia*, DC.), in *Roydsia*, *Crataeva*, *Ritschiea fragrans*, R. Br. and *Tovaria pendula*, Ruiz et Pav. Apart from this broad differentiation of the mesophyll considerable differences are found in the more or less abundant development of palisade-parenchyma, in the length of the palisade-cells, in the dense or loose nature of the spongy parenchyma, and so on—features which, with the necessary caution, may be made use of for specific diagnosis. In this connexion it ought also to be mentioned that the whole of the mesophyll is sometimes formed by palisade-tissue, which is then usually (*Capparis galeata*, Fres. and *Cadaba glandulosa*, Forsk.) composed of short cells. According to Radlkofer, a peculiar fissuring of the tissue on the drying of the leaves causes the appearance of fine transparent striae in certain species of *Capparis* (*C. callosa*, Bl., *C. flexuosa*, Bl., *C. jamaicensis*, Jacq., *C. isthmensis*, Eichl., *C. micracantha*, DC., and *C. odoratissima*, Jacq.), *Morisonia* (*M. Imrayi*, Griseb.), and *Forchhammeria* (*F. apiocarpa*, Radlk. and *F. pallida*, Liebm.). Another noteworthy feature, which is of value in specific diagnosis, is the occurrence of sclerenchyma in the leaf-tissue. In *Capparis zeylanica*, L. the lowest cell-layer of the spongy tissue is sclerosed (Fig. 18, *A*). Much more frequently solitary sclerenchyma-cells are found in the mesophyll; they are of varied shape. Isodiametric, unbranched, or almost unbranched stone-cells have been observed in the mesophyll of *Niebuhria Caffra*, DC., *Cadaba rotundifolia*, Forsk., *Capparis floribunda*, Wight, and *C. polyantha*, Tr. et Pl. *Thylachium heterophyllum*, Juss., *Niebuhria pedunculosa*, Hochst., *Capparis parviflora*, Boiss., and *C. aphylla*, Roth. possess spicular cells, which are branched in all directions. In another series of species the sclerenchyma-cells are elongated in the same direction as the palisade-cells (Fig. 18, *B*), and at the same time vary in length and are slightly branched or unbranched; e.g. in *Boscia salicifolia*, Oliv., *B. urens*, Welw., *Capparis arborea*, F. v. Müll., *C. callosa*, Bl., *C. jamaicensis*, Jacq., *C. longifolia*, Sw., *C. lucida*, Banks, *C. nobilis*, F. v. Müll., *C. odoratissima*, Jacq., *C. oleoides*, Burch., and *C. Rothii*, Oliv. Sclerenchyma-cells, likewise elongated in the same direction as the palisade-cells, some having almost the appearance of fibres, with branched extremities, are found in *Niebuhria linearis*, DC., *Courbonia glauca*, Brongn., *Boscia microphylla*, Oliv., *B. octandra*, Hochst., *Capparis isthmensis*, Eichl., and *C. Thozetiana*, F. v. Müll. Lastly, sclerenchyma-fibres, running more or less irregularly in the leaf-tissue, occur in *Boscia reticulata*, Hochst., *Cadaba glandulosa*, Forsk., *C. longifolia*, DC., *Capparis pedunculosa*, Wall.,

C. verrucosa, Jacq., and *C. Yco*, Mart. Most of the sclerenchyma-cells in question are of the nature of mesophyll-cells. An exception is afforded by the sclerenchyma-cells of *Capparis jamaicensis*, which are elongated in the same direction as the palisade-cells and intrude their upper ends between the epidermal cells; Radlkofer has proved developmentally that these elements arise from epidermal cells. In other species also of *Capparis*, viz. *C. isthmensis*, *C. odoratissima*, *C. Yco*, *C. domingensis* (Fig. 18, *C*), &c., a similar origin is indicated by the penetration of the sclerenchyma-cells between the epidermal cells and by the occasional very regular grouping of the latter in the form of a rosette around the terminal part of the spicular cell, which sometimes projects as a short hair. In *C. domingensis*, only part of the body of the sclerenchyma-cell lies in the mesophyll; the other part projects like a hair above the epidermis.

In the Cappareae the **epidermal cells** for the most part have straight lateral walls, rarely however these walls are somewhat strongly curved (*Steriphoma paradoxum*, Endl., *Cadaba longifolia*, DC., *Capparis callosa*, Bl., and *C. frondosa*, Jacq.); both these structural features occur in the Cleomeae also. The cuticle is either smooth or frequently it is striated. According to present experience, it appears that greater systematic value must be attributed to the striation of the cuticle (which is sometimes carried to the extent of formation of cuticular ridges) in the Capparideae than elsewhere. Thus, according to Radlkofer, a wavily nodular striation of the cuticle on the lower side of the leaf has proved to be characteristic of the species of *Capparis* belonging to the section *Quadrella*, while a smooth epidermis is found in the species of the section *Breyniastrum*. Strong striation of the cuticle also occurs, according to Vesque, in certain Cleomeae, e.g. in *Isomeris* and *Wislizenia refracta*, Engelm. Granulation of the cuticle is rarely present in the Order, as for example in *Capparis Sepiaria*, L. on the upper side of the leaf, and in *Cleome glauca*; wart-like inequalities of the cuticle have been observed only in *Capparis umbellata*, R. Br. Formation of epidermal papillae occurs on the lower side of the leaf in *Crataeva religiosa*, Forst., and *C. Nurvala*, Hamilt., and also in *Isomeris* and in *Wislizenia refracta*, Engelm. In *Courbonia glauca*, Brongn. only some of the epidermal cells (forming groups of a few cells each) are arched outwards as papillae, and thus to some extent recall the differentiation of the epidermis occurring so frequently in the Cruciferae. Further, in *Capparis Yco*, Mart., a considerable number of epidermal cells are sclerosed; in *C. frondosa*, Jacq., the whole, in *C. micracantha*, DC., only the margin of the outer wall is punctate. *Morisonia americana*, L. is distinguished by an extremely small-celled epidermis. In certain members of the Order **hypoderm** is developed, e.g. in *Forchhammeria* and in some species of *Capparis* (*C. angustifolia*, H. B. K., *C. arborea*, F. v. Müll, *C. lucida*, Banks, *C. nobilis*, F. v. Müll., *C. Roxburghii*, DC., *C. scabrida*, H. B. K.). The hypoderm is usually only 1–2 cells thick, in *C. scabrida* 5 cells thick; the hypoderm of *Capparis nobilis*, which is 1–2 cells thick, contains stone-cells. Gelatinization of the epidermis of the leaf has not been observed in any species; I shall return later to the crystalline contents of the epidermis when discussing crystals in general.

In mature leaves the **stomata** are surrounded by usually four or even more irregularly arranged epidermal cells of ordinary shape. Nevertheless, according to Vesque, a definite type is originally present, which is obscured in the mature leaf. Thus the initial cell first divides by a division-wall into two daughter-cells of equal size; then in one of the latter the formation of a division-wall at right angles to the first wall takes place; of the last-formed cells one is the mother-cell of the two guard-cells, a division-wall arising in it parallel to the first wall. As regards the distribution of the stomata, the latter are usually found on both surfaces in centrically constructed leaves, but for the most part only on the lower side in bifacial leaves. Exceptions to this rule, however, occur. Thus, for example, the centric leaves of *Capparis Mariana*,

Jacq., and of *Boscia microphylla*, Oliv., have stomata only on their lower sides; the bifacial leaves of *Niebuhria linearis*, DC., *Maerua angustifolia*, A. Rich. and *Capparis Nummularia*, DC. have stomata on both sides, though less numerous on the upper side.

The smaller **veins** of the leaf are almost always embedded in the mesophyll. They are accompanied by sclerenchyma, resembling bast-fibres, which may be either weakly or strongly developed, or by collenchyma; in many cases there is no mechanical tissue in the veins. It may be remarked at once that the last statement also holds good for the vascular bundles in the principal vein and in the petiole. True vertical transcurrence of the smaller veins has been observed in *Morisonia* only; the vascular system of these veins is enclosed by sclerenchyma, which resembles hard bast-fibres, and is continued above and below in the form of plates reaching the epidermis on both sides, and spread out laterally beneath the epidermis in the form of a T. The smaller veins of *Boscia reticulata*, Hochst., of *Capparis Yco*, Mart., and of *C. zeylanica*, L. may also be described as vertically transcurrent in consequence of the development of sclerenchyma on the upper and lower sides of the vascular system. The terminations of the veins are developed in the form of enlarged pitted or spirally striate tracheides, serving as water-reservoirs (what are called enlarged terminal tracheides), in the meshes of the veins in species belonging to the genera *Capparis* (*C. galeata*, Fres., Fig. 18, *D*, *C. Roxburghii*, DC., *C. rupestris*, Sibth. et Sm., *C. spinosa*, L.), and *Cadaba* (*C. heterotricha*, Stocks).

The vascular bundles in the **midrib** are mostly arranged in the form of a straight band or of an arc projecting convexly towards the lower side. In *Steriphoma*, *Morisonia*, and *Capparis Pachaca*, H.B.K., in addition to this arc, there is a second one inversely orientated as regards the position of xylem and phloem, whereby the differentiation of a ring of vascular bundles is indicated. In *Capparis scabrida*, H. B. K., between the lower arc of vascular bundles and the upper inversely orientated one, a third arc is intercalated with the same position of xylem and phloem as in the first. Lastly, the transverse section of the **petiole** shows either an arc or a ring of vascular bundles. The last-mentioned features can in general only be employed for specific diagnosis.

The **crystalline contents** found in the Capparideae require a more detailed investigation with regard to their chemical nature. For hitherto in nearly all cases the configuration of the crystalline elements has alone been described. In this connexion the fact must be emphasized, that ordinary large solitary crystals have only very rarely been observed in the Order (cortex of species of *Forchhammeria*); more frequently clustered crystals (see Fig. 18, *A* and *D*) are found, and besides these smaller lozenge-shaped or prismatic crystals, some of which, when in the right position, show a six-angled shape like the conventional 'star' as painted on a signboard (Fig. 18, *E–F*). The following statements may be made regarding the distribution of the crystalline elements. Fairly large clustered crystals occupy nearly all the cells of the mesophyll in *Capparis pubiflora*, DC. These are less numerous in the mesophyll of *Capparis zeylanica*, L.; in *C. heteracantha*, DC. several clustered crystals are found in the same palisade-cell. Prismatic solitary crystals occur abundantly in the mesophyll, for example, in *Capparis Sepiaria*, L., in *Cadaba glandulosa*, Forsk., and *C. heterotricha*, Stocks. The latter are very widely distributed in the epidermis of the leaf.

A crystal-containing epidermis is described as occurring in the following Capparideae by Vesque and Radlkofer: *Morisonia americana*, L.; *Niebuhria pedunculosa*, Hochst.; *Maerua angustifolia*, A. Rich.; *Cadaba rotundifolia*, Forsk.; *Capparis Breynia*, Jacq., *C. Cynophallophora*, L., *C. divaricata*, Lam., *C. Guaya quilensis*, H. B. K., *C. Heyneana*, Wall., *C. jamaicensis*, Jacq., *C. linearis*, Jacq., *C. mollis*, H. B. K., *C. odoratissima*, Jacq., *C. pendula*, Tr. et Pl., *C. polyantha*, Tr. et Pl.,

C. scabrida, H. B. K., *C. tenuisiliqua*, Jacq., *C. verrucosa*, Jacq., *C. Yco*, Mart., *C. zeylanica*, L.; *Forchhammeria*.

As to the chemical nature of the prismatic crystals it should be mentioned, in accordance with the investigations of Radlkofer, that only some of these crystals (e.g. those situated in the epidermis in *Forchhammeria* and *Capparis subcordata*, Span. and those present in the interior of the leaf of *Capparis multiflora*, Hook. f. et Th., *C. olacifolia*, Hook. f. et Th., *C. pubiflora*, DC., and *C. Zeyheri*, Turcz.) consist of oxalate of lime; in other species of *Capparis* they prove to be composed of sulphate of lime. The latter is the case, e.g., in *Capparis jamaicensis*, Jacq. and the remaining species of the section *Quadrella* (*C. isthmensis*, Eichl., *C. longifolia*, Sw., and *C. odoratissima*, Jacq.).

The fact that the last-mentioned crystals consist of gypsum, may be easily proved by a few micro-chemical reactions, viz. solubility of the crystals in water; conversion of the crystals by means of oxalate of ammonia into oxalate of lime, and determination of the latter in the well-known way by means of acetic acid, hydrochloric acid and sulphuric acid; lastly, conversion of the crystals into barium sulphate by barium chloride. According to the experience of Radlkofer in *Capparis jamaicensis*, the abundance of gypsum-crystals in the epidermis occasionally shows considerable variation, and further, gypsum-crystals are sometimes wanting in this species, and are then replaced by yellowish sphaero-crystalline masses of gypsum, resembling drops of oil; it would thus appear that it is not so much the occurrence of gypsum-crystals in the epidermis, but rather the presence of the gypsum forming them, which is the essential and characteristic feature. It is not superfluous to note that the statements made with regard to the occurrence of crystals and of spheres of gypsum refer to dried herbarium-material, but it should be added that gypsum and gypsum-spheres have also been observed in the fully developed living leaf. It thus remains an open question whether this may not always be the case and whether deposition of gypsum takes place at all on drying, unless its formation had been initiated during the life of the plant.

I am further able to state as an appendix to the above that a more detailed investigation on the general features and the nature of the crystals in the Order has been begun by Herr Jehlin at the suggestion of Prof. Radlkofer. As Jehlin is not at present in a position to bring his researches to a conclusion, I will briefly communicate in this paragraph the results so far arrived at. Jehlin has examined a large number of species of *Capparis* and *Cleome*. With regard to the species of *Cleome* it should firstly be mentioned, that, in these, gypsum occurs neither in the epidermis nor in the mesophyll; where a crystal-containing epidermis was met with, the crystals always consisted of oxalate of lime (*Cleome aculeata*, L., *C. aspera*, Wall., *C. gigantea*, L., *C. psoraleaefolia*, DC., *C. pubescens*, Sims., *C. pungens*, Willd., *C. scaposa*, DC., *C. spinosa*, L., *C. trachycarpa*, Klotzsch). The species of *Capparis* differ in this respect, as had already been shown by Radlkofer's researches. A large group of these species contain gypsum in the epidermis in the form of crystals or of sphaero-crystalline masses. In a second group of species gypsum is wanting in the epidermis, but in this case occurs sometimes, though not always, in the mesophyll. A third and quite small group of the species contain no gypsum, but in its place have crystals of oxalate of lime in the epidermis. To the first category of species belong: *C. Breynia*, L., *C. coccolobaefolia*, Mart., *C. corymbifera*, E. Mey., *C. Cynophallophora*, L., *C. domingensis*, Spreng., *C. ferruginea*, L., *C. frondosa*, Jacq., *C. galeata*, Fres., *C. grandis*, L., *C. incana*, H. B. K., *C. isthmensis*, Eichl., *C. jamaicensis*, Jacq., *C. lineata*, Pers. var. *glabrescens*, *C. micracantha*, DC., *C. odoratissima*, Jacq., *C. oleoides*, Burch., *C. oxysepala*, Wright., *C. sabiaefolia*, Hook. fil. et Thoms., *C. tenuisiliqua*, Jacq., *C. Yco*, Mart.; to the second category belong: *C. divaricata*, Lam., *C. flexuosa*, Bl., *C. grandiflora*, Wall., *C. lineata*, Domb., *C. horrida*, L., *C. membranifolia*, Kurz, *C. multiflora*, Hook. fil. et Th., *C. olacifolia*, Hook. fil. et Th., *C. Rothii*, Oliv., *C. Roxburghii*, DC., *C. Sepiaria*, L., *C. spinosa*, L., *C. tenera*, Dalz., *C. tomentosa*, Lam., *C. viminea*, Hook. fil. et Th.; lastly, to the third category belong: *C. formosa*, Dalz., *C. Heyneana*, Wall., *C. subcordata*, Span., and *C. zeylanica*, L.[1]

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[1] The terminology of the species is that of the Herb. Monacense.

In connexion with the gypsum-crystals just discussed it may further be mentioned, that in other genera besides *Capparis*, namely, in *Cladostemon paradoxus*, A. Br. et Vatke and in *Thylachium panduraeforme*, Juss., Blenk has also observed sphaero-crystalline masses, which likewise consist of gypsum and are situated in wart-like elevations on the leaf; and also that, according to Radlkofer, gypsum appears to be replaced by a double salt of lime and magnesium, which is deposited in spherical masses, in certain species of the genus *Capparis* (*C. flexuosa*, Bl., *C. rupestris*, Sibth. et Sm., and *C. subcordata*, Span.).

Internal **secretory organs** occur in the form of cells, which are filled with proteid-bearing contents, staining yellow with iodine and distinctly showing Millon's reaction. They are best described as myrosin-cells, because myrosin has been recognized in them by Guignard as a specially characteristic component of their contents. In the root they occur in the primary and secondary cortex as well as in the pith; they are found in the same tissues in the stem; in the leaf they are either free in the mesophyll, in both palisade and spongy tissue, or they only accompany the vascular bundles of the veins, bordering closely on the sclerenchyma-sheath of the latter; lastly, they are also specially abundant (according to Guignard) in the floral organs [1]. In shape these elements are usually only slightly or not at all distinguished from the adjacent cells; in the cortex alone they are sometimes elongated in the vertical direction and are arranged in groups of a few placed vertically one above another.

The myrosin-cells were first demonstrated by Heinricher in some species of *Capparis* (*C. spinosa* and two species described as *C. aegyptiaca* and *C. latisiliqua*) in the mesophyll as well as in the pith and cortex of the branches, and were named by him 'proteid-sacs' on account of the proteid-reactions of their contents. The thin-walled cells, with contents staining yellow with watery iodine-solution, observed by Radlkofer in the neighbourhood of the vascular bundles of the veins, are, according to the researches of Guignard, identical with these proteid-sacs and hence also with the myrosin-cells. Radlkofer met with them in *Capparis jamaicensis* and subsequently Jehlin, in a further survey made at Radlkofer's suggestion, found them in a fairly large number of species of this genus [2]. Guignard also observed these cells in *Capparis ferruginea*, L., where they were seen by Jehlin, and further in *C. frondosa*, L., in a species described as *C. platycarpa* and in *C. saligna*, Vahl, and called them myrosin-cells.

In this connexion the remaining statements of Guignard as to the occurrence of the myrosin-cells may be appended. It is specially important, that the myrosin-cells are not restricted to the genus *Capparis*, but also occur in other genera of the Order, firstly in the genus *Cleome* (in this case contrary to a statement of Heinricher) and also in *Gynandropsis* and *Polanisia*. Guignard observed myrosin-cells: in *Capparis spinosa* in the pith and cortex of the root and stem as well as in the mesophyll; in *Cleome arborea*, H. B. K. in the cortex of branch and root as well as in the leaf-tissue; in *Cleome alliodora*, 'H. B.' in the cortex of branch and root; in *Gynandropsis speciosa*, DC. in the cortex of branch and root; in *Polanisia graveolens* 'DC.' in the cortex of the branch. More thorough investigation is required to determine how widely myrosin-cells are distributed in the Order.

Similarly the question of relation between the thin-walled cells (first observed by Blenk) and the myrosin-cells has still to be solved; the former cells are filled

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[1] According to Guignard myrosin is also present in the seed (*Capparis spinosa*), but in small quantity; the myrosin-cells are here unrecognizable histologically.

[2] These are: *Capparis coccolobaefolia*, *C. corymbifera*, *C. Cynophallophora*, *C. divaricata*, *C. ferruginea*, *C. formosa*, *C. galeata*, *C. grandis*, *C. incana*, *C. lineata*, *C. lineata* var. *glabrescens*, *C. odoratissima*, *C. spinosa*, *C. tomentosa*. In the following species, on the other hand, they were not observed: *C. Breynia*, *C. Cynophallophora* ex parte, *C. domingensis*, *C. flexuosa*, *C. frondosa*, *C. grandiflora*, *C. Heyneana*, *C. horrida*, *C. isthmensis*, *C. membranifolia*, *C. micracantha*, *C. multiflora*, *C. olacifolia*, *C. oleoides*, *C. oxysepala*, *C. Rothii*, *C. Roxburghii*, *C. sabiaefolia*, *C. Sepiaria*, *C. subcordata*, *C. tenera*, *C. tenuisiliqua*, *C. viminea*, *C. Yco*. (For the authors' names see the enumeration of the species investigated by Jehlin with regard to the features of their crystals.)

with special contents and surround the bundles of the veins of the leaf in the form of a sheath in all investigated Cleomeae (species of the genera *Dactylaena, Cleome, Buhsea, Physostemon, Cleomella, Cyrbasium, Isomeris, Polanisia, Gynandropsis*). It may be noted here, that Guignard also observed the cells in question in *Cleome alliodora*, H. B., that he described their contents as proteiniferous, but left the question of their relation to the myrosin-cells open. Vesque's statement, that mucilage-cells sometimes occur in members of the tribe Cappareae in the mesophyll or in the parenchyma of the veins or petiole, likewise needs further examination as to its correctness; Vesque figures these mucilage-cells for the petiole of *Capparis heteracantha*, DC. It seems possible that this is due to confusion with myrosin-cells.

The following facts should be mentioned regarding the different forms of **hairs** in the Capparideae, and their distribution, as they were only shortly treated under the general characters. Firstly, simple unicellular hairs occur in many members of the Order. In one series of species these hairs are short, and at the same time usually have thick walls, more rarely wide lumina (*Maerua scabra*, Camb., *M. senegalensis*, R. Br., *M. uniflora*, Vahl; *Boscia octandra*, Hochst., *B. salicifolia*, Oliv.; *Capparis Cynophallophora*, L., *C. linearis*, Jacq.). *Capparis mollis*, H. B. K., *Roydsia parviflora*, Griff., and *R. suaveolens*, Roxb. have longer unicellular hairs; in the first plant they have a wide lumen and show a striated surface; in the other two they are thick-walled. *Capparis Rothii*, Oliv. has ribbon-shaped unicellular hairs. The long unicellular hairs of *Boscia urens*, Welw. are surrounded at their base by subsidiary cells, which project like a pedestal above the level of the other epidermal cells. Further, the unicellular hairs, which are peculiar to certain species of *Capparis* (*C. galeata*, Fres., *C. Mariana*, Jacq., *C. Nummularia*, DC., *C. rupestris*, Sibth. et Sm., *C. sarmentosa*, F. v. M., *C. spinosa*, L., Fig. 19, *A*), are quite characteristic. These are thin-walled, wide-lumened, ascus-shaped hairs, which are pointed at their ends, attain their greatest breadth above the middle-point of their length, and from this point are narrowed gradually towards the base. Then there also occur unicellular Malpighian hairs (Fig. 19, *B*), namely in *Capparis pubiflora*, DC., *C. quiniflora*, DC., and *C. Zeyheri*, Turcz. If one imagines more than two arms to be developed in these Malpighian hairs, unicellular, branched, many-rayed hairs (Fig. 19, *C*) would be produced. These have been observed in *Capparis avicenniaefolia*, H. B. K., *C. dealbata*, DC., *C. diversifolia*, W. et A., *C. erythrocarpos*, Isert, *C. foetida*, Bl., *C. Heyneana*, Wall., *C. horrida*, L., *C. Moonii*, Wight, *C. stylosa*, DC., *C. tenera*, Dalz., and *C. zeylanica*, L.; they are usually thin-walled, more rarely (*C. diversifolia* and *C. tenera*) thick-walled. Besides the unicellular trichomes referred to so far, simple uniseriate hairs also occur in the Order, namely in *Maerua aethiopica*, Oliv., and in many species of *Capparis*, e.g. *C. citrifolia*, Lam., *C. lanceolaris*, DC., and *C. tomentosa*, Lam. They are usually long and have fairly thick walls, more rarely (*C. Thozetiana*, F. v. Müll.) they are short, and consist of a varied number of cells. Unicellular and uniseriate trichomes occurring side by side have been demonstrated in *C. polymorpha*, A. Rich. Emergences resembling shaggy hairs are rare. The following belong to this category: the rather long shaggy hairs of *Cadaba capparoides*, DC. consisting of a few bicellular cell-rows, each of which terminates in an acutely papillose cell (Fig. 19, *D*); the short analogously constituted shaggy hairs of *Morisonia americana*, L.; and the hemispherical, multicellular emergences of *Capparis verrucosa*, Jacq., on which separate 1–3-celled trichomes are inserted (Fig. 19, *E*). Like the shaggy hairs, multicellular stellate hairs are also uncommon. The latter consist of a multiseriate pedestal, on the apex of which are inserted a variable number of ray-cells, which either lie in one plane, or radiate in different directions. To the first category of these stellate hairs, viz. those with the ray-cells lying in the same plane, belong those of *Steriphoma paradoxum*, Endl. (Fig. 19, *F–G*) and *S. peruvianum*, Spruce. A specially note-

worthy feature in these hairs is that above the expanded rays a layer of cells is found presenting the form of very short rays only differentiated as papillae (a so-called upper scale, 'oberes Schülferchen'). Owing to this latter feature a double connecting link, so to speak, is formed, on the one hand with the small peltate scales of the Capparideae, to be discussed later, on the

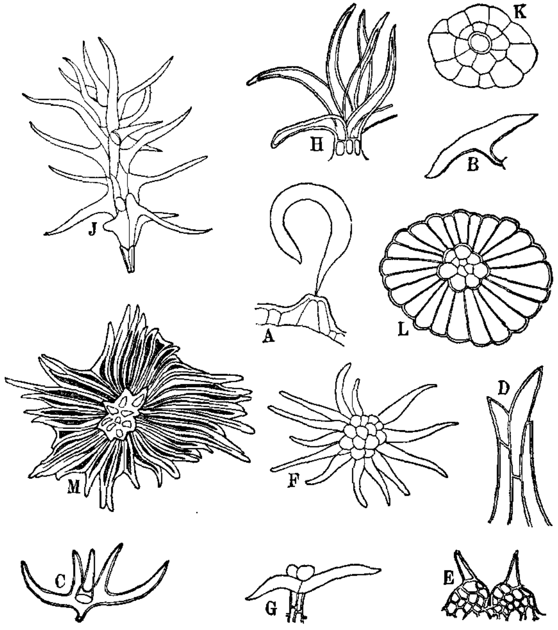

FIG. 19. Hairy covering of the Capparideae: A, *Capparis spinosa*, L.; B, *C. quinifolia*, DC.; C, *C. zeylanica*, L.; D, *Cadaba capparoides*, DC.; E, *Capparis verrucosa*, Jacq.; F–G, *Steriphoma paradoxum*, Endl.; H, *Capparis ferruginea*, L.; J, *C. domingensis*, Spreng.; K, *Cadaba farinosa*, Forsk.; L, *Atamisquea emarginata*, Miers; M, *Capparis Breynia*, Jacq.—J, Original; the rest after Vesque.

other hand, with the second category of stellate hairs, the brush-shaped type, in which the ray-cells radiate in all directions (Fig. 19, *H*). The latter have only been observed in species of *Capparis* (*C. angustifolia*, H. B. K., *C. Breynia*, Jacq., *C. crotonoides*, H. B. K., *C. detonsa*, Tr. et Pl., *C. ferruginea*, L., *C. incana*, H. B. K., *C. scabrida*, H. B. K., *C. Yco*, Mart.). With the brush-shaped stellate hairs one may also class the candelabra-hairs of *Capparis domin-*

gensis, Spreng. (Fig. 19, *J*), transitions to which occur in *C. ferruginea*. I now come to speak of the peltate hairs; among these may be classed the trichomes of *Cadaba heterotricha*, Stocks (cf. Vesque, Eph. Tab. XIX), in which the pointed and rather thick-walled cells are only united for half their length, and form a six-rayed star, on which, to judge by Vesque's figure, a second smaller plate of cells, a so-called upper scale, is inserted. Other species of *Cadaba* have differently constituted scales. In these the margin of the shield has an almost circular outline, and is slightly crenate in consequence of slight projection of the cells of the shield; in surface-view the shield consists either of a single ring of cells (*Cadaba longifolia*, DC.) or a double ring (*C. farinosa*, Forsk., Fig. 19, *K*); the upper scale is absent. The peltate hairs of *Atamisquea emarginata*, Miers (Fig. 19, *L*) agree with those of *Cadaba*, which have just been described, in their form and the nature of the margin, but possess a distinct upper scale. The latter occurs quite generally in the peltate hairs of the species of *Capparis* (*C. Breynia*, Fig. 19, *M*, *C. jamaicensis*, *C. isthmensis*, *C. longifolia*, and *C. odoratissima*) as well as in those of *Morisonia americana*, L., and *M. Imrayi*, Griseb.; the thick-walled cells of the shields of these hairs project like rays at the margin.

Glandular hairs and glandular shaggy hairs are rare in the tribe Cappareae, but are common in the Cleomeae. The glandular hairs of *Cadaba glandulosa*, Forsk. have a uni- to multiseriate stalk and a few- to many-celled head. In the tribe Cleomeae they are variously constructed, being either sessile or stalked, and in the latter case provided with a uni- or multiseriate stalk, and furnished with a unicellular or multicellular head.

3. Structure of the Axis. The structure of the axis of the Capparideae has so far been little investigated. The following facts should be quoted with regard to the anatomy of the **cortex**, chiefly from Möller[1]. The cork arises either from the epidermis (*Crataeva*) or from the outer and partly also from deeper layers of the primary cortex (*Capparis*). In *Capparis* the cork-cells have thin walls, in *Crataeva* they become sclerosed on one side. Formation of aerenchyma is stated by H. Schenck to occur in the lower part of the stem of specimens of *Cleome spinosa* from swampy habitats; the formative tissue of this aerenchyma arises in the innermost part of the primary cortex. In *Crataeva* the primary cortex contains groups of stone-cells; in the species of *Forchhammeria* it contains extraordinarily numerous stone-cells, the cavities of which are for the most part filled with large solitary crystals of oxalate of lime. In *Capparis frondosa* the primary cortex at an early stage contains a closed ring of stone-cells. The pericycle is formed by groups of bast-fibres, which are united by intervening stone-cells into incomplete (*Capparis*, *Crataeva*) or complete (*Roydsia*) sclerenchymatous rings. Bast-fibres are wanting in the secondary bast, and stone cells occur in the latter only in the tissue of the medullary rays.

In the species investigated by me[2] the **xylem** shows medullary rays from two to four cells broad; according to H. Schenck, the medullary rays of the wood of *Capparis lineata*, Domb. have a considerably greater breadth. The vessels possess lumina of various sizes (maximum diameter, ·036–·078 mm.). On their walls the vessels bear bordered pits of varied size, and these are also present in contact with medullary-ray-parenchyma. The transverse walls of the vessels have simple perforations. Spiral thickening of the wall has been observed in the pitted vessels of *Cleome rosea*. Wood-parenchyma is found in the neighbourhood of the vessels, and sometimes in no small amount. The wood-prosenchyma has simple pits.

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[1] Möller only investigated *Capparis frondosa*, L., *Crataeva Murvala*, Hamilt., *C. religiosa*, Forst. and *C. Tapia*, L.

[2] These are: *Capparis jamaicensis*, Jacq., *Cadaba farinosa*, Forsk., *Atamisquea emarginata*, Miers, *Cleome rosea*, Vahl, *Isomeris arborea*, Nutt.

Anomalous stem-structure has been met with in the genera *Maerua*, *Roydsia*, *Cadaba*, and *Forchhammeria* in the form of successive rings of growth. In *Maerua uniflora*, according to De Bary, the secondary rings of vascular bundles arise intrafascicularly, in the zone of bast itself; in *Forchhammeria trifoliata*, Radlk., *Maerua oblongifolia*, A. Rich., and *Roydsia*[1], according to Radlkofer, they arise on the inner side of the sclerenchyma of the pericycle. *Forchhammeria apiocarpa*, Radlk., and *F. pallida*, Liebm., according to Radlkofer, behave differently, for in them the secondary rings of growth take their origin on the outer side of the pericyclic sclerenchyma. The primary hard bast of the original ring of vascular bundles here becomes completely enclosed by the first ring of growth; the latter contains no hard bast. The formation of the secondary bundle-rings of *Cadaba glandulosa* likewise takes place in the outer cortex according to Krüger. To complete the review of the anomalous axes, which have been described in detail, it may be added that the successive zones of soft bast form continuous rings in the transverse section in *Maerua* and *Forchhammeria*, but in *Roydsia* they are broken up into separate groups of soft bast by the lignified, fairly broad medullary rays, which traverse the whole xylem-mass radially. Lastly, it may also be mentioned, that the *Capparis*-lianes investigated by H. Schenck have a xylem-mass of normal structure.

Addendum. According to Lagerheim, the genus *Tovaria*, which is usually doubtfully appended to the Capparideae, possesses no noteworthy anatomical features, by which the question of its affinity might be decided, except 'large idioblasts apparently containing mucilage,' which are situated in the primary cortex.

Literature: Möller, Holzanatomie, Denkschr. Wiener Akad. 1876, pp. 73, 74 and 369, 370.—De Bary, Vergl. Anat., 1877, p. 606.—Möller, Rindenanat., 1882, pp. 234–6.—Vesque, Monogr. anat. et descript. de la tribu des Capparées, Ann. sc. nat., sér. 6, t. xiii, 1882, pp. 47–143, Pl. i, ii.—Vesque, Nouv. Arch. Mus. d'hist. nat., sér. 2, t. v, 1882–3, pp. 304–11.—Blenk, Flora, 1884, p. 102 et seq., separate copy, pp. 16–20.—[Filarszky, Syst. Stell., Anat. etc. der Cleomeae, Hungarian, Budapest, 1884, 48 pp. and 6 Tab.]—Krüger, Anomale Holzbild., Diss., Leipzig and Nauen, 1884, p. 21.—Radlkofer, *Forchhammeria*, Sitz.-Ber. Münch. Akad. 1884, p. 58 et seq. and *Capparis*-Arten, Sitz.-Ber. Münch. Akad. 1884, p. 101 et seq.—Volkens, Standort u. anat. Bau, Jahrb. Berliner Gart. 1884, p. 32 et seq.—Solereder, Holzstruktur, 1885, pp. 62, 63.—O. Bachmann, Schildhaare, Flora 1886, separate copy, pp. 29–31 and Taf. 1, Fig. 20.—Heinricher, Mitteil. bot. Inst. Graz, Heft 1, 1886, p. 46.—Radlkofer, Sitz.-Ber. Münch. Akad. 1886, p. 301.—Radlkofer, *Capparis*-Arten II. Sitz.-Ber. Münch. Akad. 1887, p. 365 et seq.—Vesque, Epharmosis I, Vincennes, 1887, 10 pp. and 77 Tab.—Volkens, Aegypt.-arab. Wüste, 1887, pp. 96, 97 and Tab. vi and ix.—H. Schenck, Aërenchym, Pringsheim Jahrb., Bd. xx, 1889, p. 550.—Pax, in Natürl. Pflanzenfam., iii. Teil, Abt. 2, 1891, p. 210 et seq.—Lagerheim, Tovariaceen, Sitz.-Ber. deutsch. bot. Gesellsch. 1892, pp. 168, 169.—Guignard, Principes actifs chez les Capparidacées etc., Journal de bot., t. vii, 1893, pp. 350–64.—H. Schenck, Anat. der Lianen, 1893, pp. 70, 71.—Radlkofer, Field Columb. Mus. Chicago, vol. i, n. 4, 1898, p. 399.

RESEDACEAE.

The anatomy of this Order is chiefly known through the researches of Vesque[2] and Volkens[3]. For the diagnosis of the Order the following characters may be pointed out: simple perforations of the vessels; wood-prosenchyma having simple pits; lack of special stomatal apparatus; absence of crystals of oxalate of lime, as well as of sclerenchymatous tissue-elements in the veins of the leaf; occurrence of simple unicellular trichomes mostly rounded off at the apex, while glandular hairs are absent. The occurrence of myrosin-cells in the genus *Reseda* and the histological differentiation of the epidermis of the leaf (Fig. 20, *A–B*) in this genus, which is similar to that found in the

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[1] I have met with anomalous stem-structure throughout in the species contained in the Herb. Monac. (*R. floribunda*, Planch., *R. parviflora*, Griff., and *R. suaveolens*, Roxb.).

[2] Vesque, Nouv. Arch. Mus. d'hist. nat., sér. 2, t. v, 1882–3, pp. 311–14 and Pl. 19.

[3] Volkens, Aegypt.-arab. Wüste, 1887, pp. 98–101 and Taf. iii and vii.

Cruciferae, is an anatomical indication of the relationship of the Resedaceae to the Cruciferae, and in part, as regards the myrosin-cells, to the Capparideae also.

The following may be mentioned as to the more detailed features of the leaf-structure. The mesophyll shows either no differentiation or indistinct bifacial structure or lastly, centric structure, the latter, e.g. in *Ochradenus baccatus*, Del., *Oligomeris subulata*, Webb, &c. The leaves with centric structure contain colourless parenchyma in the middle of the leaf or at any rate parenchyma which is poor in chlorophyll (aqueous tissue). In plants with reduced leaves, such as *Ochradenus baccatus*, the primary cortex takes over the assimilatory function of the mesophyll and in correspondence with this circumstance consists of palisade-cells. The lateral walls of the **epidermal cells** are mostly undulated, more rarely straight. Gelatinization of the inner wall occurs in the epidermis of the leaf of *Caylusea canescens*, St. Hil., *Ochradenus baccatus*, Del.[1], *Oligomeris subulata* Webb (Fig. 20, *A–B*), *Reseda arabica*, Boiss., *R. Boissieri*, Müll. Arg., *R. decursiva*, Forsk. and *R. pruinosa*, Del. In certain species there is a still more pronounced histological differentiation of the epidermis (Fig. 20, *A–B*), inasmuch as certain epidermal cells are specially distinguished by their form and size from the remaining cells, and consequently strike the eye. Large epidermal cells of this kind occur firstly in all the species of *Reseda* named above; in *R. arabica* they project as papillae above the leaf-surface; in *R. pruinosa* they are so large that they can be seen with the naked eye, and the whole plant in the living condition appears as if covered with little drops of water. Further, the same large cells, which project as papillae and serve for the storage of water, are also present in *Oligomeris subulata* (Fig. 20, *A–B*) and in *Caylusea canescens*, where they occur chiefly in the neighbourhood of the leaf-margin, exhibiting all transitions from simple papillose protrusions to long unicellular hairs. In the mature leaf the **stomata** are generally surrounded by 3–4, rarely by more, epidermal cells, which are not differentiated by their shape. According to Vesque, however, there is a definite mode of development. The mother-cell of the two guard-cells is usually cut off by the first division in an analogous manner to the course of development in the Ranunculaceae; only rarely is the first division-wall, which is U-shaped in surface-view, followed by a second. In *Reseda arabica*, *R. Boissieri*, &c., and in *Oligomeris subulata* the stomata are equally distributed on both sides of the leaf. The vascular bundles of the smaller **veins** of the leaf are embedded in the mesophyll and possess no mechanical tissue. The **petiole**[2] contains a single vascular bundle likewise

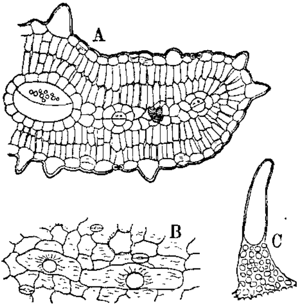

FIG. 20. A–B, *Oligomeris subulata*, Webb. A, Transverse section through the leaf; B, surface-view of the epidermis of the leaf; C, Trichome of the axis of *Reseda odorata*.—A–B, after Volkens; C, after Vesque.

[1] The mucilaginous epidermal cells of this plant were wrongly interpreted by Vesque (loc. cit., p. 313 and Pl. 19).

[2] See also Plitt, Blattstiel, Diss., Marburg, 1886, p. 24 etc.

destitute of sclerenchyma (Astrocarpus sesamoides) or, as in the grooved petioles of *Reseda alba* and other species, several vascular bundles, which are isolated and arranged in the form of an arc.

The lack of **crystals** has already been shortly mentioned above; as also have the epidermal cells with mucilaginous inner membranes. With the latter feature we may class the occurrence of mucilage-cells in the primary cortex of *Ochradenus baccatus*, their occurrence in the neighbourhood of the veins of the leaf in *Caylusea abyssinica*, Fisch. et Mey. and *C. canescens* (in the latter especially at the terminations of the bundles of the veins) and in the middle of the mesophyll of *Randonia africana*. The occurrence of myrosin in the Resedaceae now requires further discussion. It was discovered by Spatzier[1] in *Reseda*, and was investigated more closely by Guignard[2]. In the stem and root of *Reseda* the myrosin is present in special cells, which are often distinguished by their length, but always by the chemical and physical nature of their contents, which show Millon's reaction distinctly. Guignard has demonstrated these cells in the bast of the root of *Reseda alba*, *R. lutea*, *R. luteola* and *R. odorata*, and has shown them to be specially abundant in *R. lutea*; he found them also in the bast of the stem in *R. alba* and *R. lutea*, less distinctly in *R. luteola* and *R. odorata*. Moreover, the stomata of the stem as well as those of the leaf are distinguished by the presence of a considerable amount of myrosin. Distinct myrosin-cells cannot be recognized in the internal tissue of the leaf.

With regard to the **hairy covering**, the absence of glandular hairs and the occurrence of simple unicellular trichomes have already been mentioned above. The latter have wide lumina; in *Reseda odorata* they are seated on the tips of short, small-celled emergences resembling shaggy hairs (Fig. 20, *C*).

In the **stem-structure** of *Ochradenus baccatus*[3], according to Volkens, the following points are worthy of note, in addition to what has already been stated above. With increasing age of the branch a number of the epidermal cells become sclerosed. Isolated groups of bast-fibres are present at the outer limit of the bast. Besides the vessels and tracheides, the xylem contains wood-prosenchyma with simple pits, thick walls and narrow lumina, and narrow 1–2-seriate medullary rays.

CISTINEAE.

The members of this small Order are characterized anatomically by the occurrence of unicellular thick-walled hairs of special structure (for these see below and Fig. 21, *A*), which are frequently (*Cistus*, *Helianthemum*) united into star-like or brush-like tufted hairs (Fig. 21, *B–D*) or rarely into peltate hairs (Fig. 21, *E*), and by the presence of glandular hairs, which always consist of only one row of cells, but otherwise vary in structure (see Fig. 21, *F–G*). Further, stress may be laid on the following features for the diagnosis of the Order: the simple perforations of the xylem-vessels which always have small lumina; the narrow medullary rays; the bordered pitting of the wood-prosenchyma; the excretion of oxalate of lime in the form of clustered crystals; and finally, the lack of special internal secretory elements.

The structure of the **leaf**[4] is sometimes bifacial, more frequently

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[1] Myrosin in der Pfl., Pringsheim Jahrb., Bd. xxv, 1893, pp. 54, 55 and 70, 71.

[2] Localisat. des princ. act. chez les Capparidées etc., Journ. de Bot., t. vii, 1893, pp. 444–55.

[3] See also: Solereder, Holzstr., 1885, p. 63; Herbst, Markstrahlen, Bot. Centralbl., 1894, i, p. 323 et seq.; Russell, Infl. du climat méditerr., Ann. sc. nat., sér. 8, t. i, pp. 329–31.

[4] The following description of the leaf-structure is based chiefly on the statements of Vesque (loc. cit.).

centric (*Helianthemum Fumana*, Mill., &c.); in both cases the palisade-parenchyma is strongly developed. The lateral walls of the **epidermal cells** are straight or curved. In the very small leaves of *Lechea Novae-Cesareae*, Aust. the nature of the epidermis is specially striking, its cells attaining a considerable size, in correspondence with their function as water-reservoirs. I have casually observed gelatinization of the epidermis of the leaf in *Helianthemum squamatum*, Pers., and the same is described by A. Wagner for *H. alpestre* and by Grevillius for *H. oelandicum*. The **stomata** are found on both sides of the leaf in most of the species; in *Cistus* they appear to be always absent on the upper side. Special subsidiary cells are not developed in the Cistineae. A definite type of stoma, however, appears to be characteristic of the Order, but can only be clearly recognized by studying the development in young leaves; it is mostly obliterated in mature leaves; thus for the formation of the guard-cells a primordial epidermal cell in the first place divides into two daughter-cells, one of the latter then divides again, by a secondary division-wall placed at right angles to the first wall, into two daughter-cells of the second order, and one of these by a new division gives rise to the guard-cells; according to the process of division described the stoma (i.e. the two guard-cells) thus forms a quarter of the primordial mother-cell.

The small **veins** are mostly embedded in the green parenchyma or sometimes (*Helianthemum kahiricum*, Del.) in a colourless middle-layer of the leaf; the vascular bundles of the larger veins and likewise of the median veins are now and then connected with the epidermis by colourless, sometimes collenchymatous parenchyma (e.g. the larger bundles of the veins of *Cistus ladaniferus*, L. are thus connected with the upper epidermis). As a rule mechanical tissue accompanying the bundles is not developed; an exception to this is presented by *Hudsonia ericoides*, L.

In *Helianthemum* the **petiole** contains a single arc-shaped vascular bundle. In the species of *Cistus* five vascular bundles are present, and together form an arc; of these the middle bundle is the largest.

Oxalate of lime occurs in the leaf or in the parenchyma of the axis in the form of clustered crystals.

The **hairy covering** in the Cistineae is formed, as has already been stated above, by clothing and glandular hairs. The clothing hairs in the simplest case are unicellular, simple, thick-walled hairs (*Cistus*, *Hudsonia*, *Lechea*), but, according to my observations, have quite a special structure, which this Order shares with the Combretaceae. For within the base of the simple hair a second smaller hair-cell, pointed at its end and likewise thick-walled, appears to be inserted. In preparations treated with eau de Javelle, it is rendered specially evident by the yellow coloration of its wall in contrast to the white cell-wall of the hair proper. Manifestly one is here concerned with a phenomenon, which is homologous with what is called the formation of cellulose-caps in simple hairs in other Orders, and the development of the hairs in question will probably be the same as in the hairs of Combretaceae investigated by Heiden. After the wall of the hair has become thickened, and its lumen has become correspondingly narrow, the protoplasm retracts to the basal part of the hair and secretes a cellulose-cap on the side, which is directed towards the apex of the hair, the cap projecting acutely into the upper part of the latter. I have occasionally met with this doubling of the hair in the longitudinal direction in the simple unicellular trichomes of *Cistus creticus*, L. (Fig. 21, *A*), *C. ladaniferus*, L., *Lechea major*, Michx., and *Hudsonia ericoides*, L., and it is probably characteristic of the simple trichomes of the Cistineae, as has been proved (by Heiden) for the hairs of the Combretaceae. Sometimes in the same species, side by side with the simple unicellular hairs, tufted hairs may occur. These consist of a variable number of simple, unicellular, thick-walled hairs, which are

sunk side by side in the epidermis. In appearance the tufted hairs are *either brush-like, when the separate hairs stand more or less vertically,* or stellate, when the component hairs are spread out in a plane parallel to the epidermis (both kinds in *Helianthemum pilosum*). The individual hairs of these tufted hairs sometimes also show the doubling described above in the single hairs, especially when they are long (*Cistus creticus*, Fig. 21, *B*). A peculiar modification of the tufted hairs, which causes them to appear like small scales on examination with a lens, is found, according to Harms and Reiche, on *the bracts of* *Cistus ladaniferus*, L. *(Fig. 21, C–D). These small* scale-like structures are thick hemispherical cushions composed of a large number of

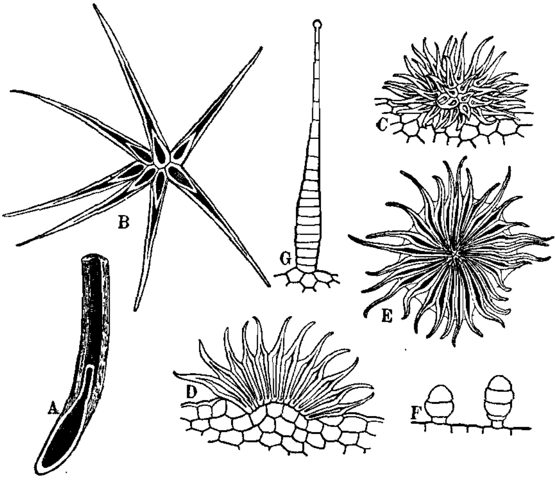

FIG. 21. Hairy covering of the Cistineae. A, Basal part of a simple hair of *Cistus creticus*, L. B, Tufted hair of *Cistus creticus*, L. C–D, Tufted hairs from the bracts of *Cistus ladaniferus*, L. E, Peltate hair of *Helianthemum squamatum*, Pers. F–G, Glandular hairs: F, *Cistus ladaniferus*, L.; G, *Cistus creticus*, L.—Original.

thick-walled hairs, which are not much elongated and are concrescent for the greater part of their length, being free only at their tips. True peltate hairs (Fig. 21, *E*) with thick-walled ray-cells, which project in a radiate manner at the margin of the shield (only some of them actually reaching the centre of the shield, the remainder approximately reaching it), have been observed in *Helianthemum squamatum*, Pers., and according to Reiche in *H. desertorum*, Willk. also.

The glandular hairs of the Cistineae have only one feature in common, namely, *that they consist of one row of cells; otherwise they differ in form,* sometimes in fact in the same species.

On the upper side of the leaf of *Cistus ladaniferus*, L., glandular hairs occur, composed so to speak solely of a sac-like glandular head, which consists of a row of few (four) short cells and is sunk in the epidermis in such a way, that the secretion formed by its cells is discharged over the epidermal surface. On the lower side of the leaf in the same plant similar few-celled, glandular hairs occur; they are, however, not sunk in the epidermis, and one can distinguish in them a 1-2-celled stalk and an ellipsoidal head of two or more cells (Fig. 21, *F*). The glandular hairs in *Helianthemum Fumana*, Mill., consist of a curved row of cells differing little from one another. In *Cistus creticus*, L., *C. villosus*, and *Helianthemum atriplicifolium*, Willd., side by side with short glands having usually a one-celled stalk and an ellipsoid, mostly 2-3-celled head, there occur more or less elongated, glandular hairs (Fig. 21, *G*), which consist of a lower, broader part (composed of a row of numerous disc-shaped cells) and a thin cylindrical terminal part of 1-4 or more cells. This terminal part extrudes a secretion (Ladanum-resin in *Cistus creticus*) between the cellulose wall and the cuticle, after the manner of the bladder-like epidermal glands.

Respecting the structure of the axis (*Cistus, Hudsonia, Lechea*) it should be mentioned that the xylem-vessels, which are scattered in a transverse section, have small lumina and simple perforations; the medullary rays are narrow; the wood-prosenchyma is fairly thick-walled and has bordered pits. Detailed investigations dealing with the cortex and the formation of cork do not exist (compare, however, Volkens' Fig. 9, Taf. I, where internal development of cork is represented in *Helianthemum kahiricum*). Small groups of hard bast are stated by Harms to occur in the cortex of *Helianthemum Fumana* and *Lechea minor*, L., solitary scattered bast-fibres in *Hudsonia ericoides*, L., while hard bast is wanting in other species.

Literature: De Bary, Vergl. Anat., 1877, p. 99.—Vesque, Nouv. Arch. Mus. d'hist. nat., sér. 2, t. v, 1882-3, pp. 315-20 and Taf. 19.—Solereder, Holzstruktur, 1885, p. 63.—Turner, Vergl. Anat. der Bixaceen, Cistaceae etc., Diss., Göttingen, 1885, p. 64.—O. Bachmann, Schildh., Flora 1886, separate copy, p. 31.—Volkens, Aegypt.-arab. Wüste, 1887, pp. 101, 102, Taf. i and viii.—A. Wagner, Sitz.-Ber. Wiener Akad., Bd. ci, Abt. 1, 1892, p. 515.—Harms, in Natürl. Pflanzenfam., iii. Teil, Abt. 6, 1895, pp. 299, 300.—Russell, Climat. méd., Ann. sc. nat., sér. 8, t. i, 1895, p. 345. —Grevillius, Engler, Bot. Jahrb., Bd. xxiii, 1896, p. 40.

VIOLARIEAE.

1. Review of the Anatomical Features. For the diagnosis of the Order with reference to the structure of the wood, stress must be laid on the following features: (*a*) the simple pitting of the wood-prosenchyma, which is frequently septate and often provided with a gelatinous membrane, and (*b*) the tendency to the formation of scalariform perforations in the vessels. The stomatal apparatus, in its mode of differentiation, belongs either to the Rubiaceous or to the Cruciferous type, or a mingling of the two types takes place. Oxalate of lime appears in the form of ordinary solitary crystals or of clustered crystals; inulin appears to be only rarely present. In many Violarieae mucilaginous epidermal cells occur; in species of *Agation, Anchietea, Corynostylis, Paypayrola* and *Viola* secretory cells with brown contents occur in the epidermis of the leaf and in the mesophyll; of the latter elements those situated in the epidermis of certain species of *Viola* are distinguished by their size and by projecting as papillae; lastly in the Sauvagesieae mucilage-sacs or mucilage-passages are found in the pith and cortex of the branches. Apart from the glandular structures of the leaf-teeth (glandular shaggy hairs in *Viola*), the hairy covering consists solely of simple, unicellular or uniseriate clothing hairs. The Sauvagesieae possess cortical vascular bundles.

2. Structure of the Leaf. The following description is based essentially

on the statements of Vesque. The **mesophyll** is mostly bifacial in structure. Centric leaf-structure, however, occurs in some cases (*Ionidium lineare* and *I. suffruticosum*). In *Viola tridentata*, Menz. and *V. muscoides*, Philippi, the mesophyll consists of homogeneous isodiametric cells, and it is only immediately above the median vein that one finds cells elongated like palisade-cells; these cells recall the hinge-cells of the grasses, and their significance has still to be determined (Reiche).

The **epidermal cells** of the leaf occasionally serve as a water-reservoir, and they are then of considerable height and size, e.g. in *Sauvagesia racemosa*, St. Hil. The gelatinization of the inner walls of the epidermal cells fulfils the same purpose in numerous species, e.g., according to Blenk in *Leonia glycycarpa*, Ruiz. et Pav. and *L. cymosa*, Mart., according to Radlkofer in many species of *Alsodeia*, and according to Krämer in species of *Viola* and other Violarieae[1]. These mucilaginous epidermal cells in some cases cause transparent dots in the leaf. Epidermal cells of this kind with mucilaginous inner walls led to an incorrect interpretation of an observation of Vesque in species of *Alsodeia* and in *Sauvagesia serpyllifolia*, Mart., described as an occurrence of division-walls in the epidermal cells of the leaf, beneath which a gummy mass is found. Further, in the epidermis of some species (*Agation violare*, A. Brongn., species of *Paypayrola*, Chilian species of *Viola*, *Anchietea salutaris*, '*Corynostylis frangulaefolia*' and *Isodendrion pyrifolium*) there occur secretory elements described by Vesque as 'cellules chargées d'une gomme-résine rougeâtre ou plus rarement jaune clair'; these elements have recently been mentioned again by Reiche as occurring in the Chilian species of *Viola* belonging to his section Rosulatae (especially *V. volcanica*, Gill. and *V. rosulata*, Poepp. et Endl.). We are here concerned with cells, which in the dry leaf are filled with resinous contents, which are mostly brown; these elements usually only differ from the neighbouring cells in their contents and not in size; they are sometimes (e.g. in *Anchietea salutaris*), however, visible as small brown spots even on inspection of the leaf with a lens. Their number varies, sometimes (*Paypayrola guianensis*, Aubl.) almost the whole epidermis is formed by the cells in question. They attain a fairly considerable size in *Viola rosulata*, and a still greater size in *Viola volcanica*, in which they project like papillae above the level of the epidermis, reach a diameter of ·03 mm., are elongated to a tubular shape, and consequently are perceptible as brown striae on the lower side of the leaf. In the species cited the same brown cells also occur in the mesophyll, being more frequent in the palisade-tissue and in the lower layers of the spongy tissue than in the middle layers of the leaf. Sphaerocrystalline masses of an organic substance, the nature of which is not more definitely known, have been met with in the epidermal cells of the upper side of the leaf of *Alsodeia castanaefolia* and *A. guianensis*, as well as of *Agation violare*. The **cuticle** is mostly thin, rarely (*Viola Cotyledon*) thick; as a rule, it is smooth or faintly striate. A stronger striation has been observed in *Scyphellandra virgata* and *Viola volcanica*; in *Hymenanthera* and *Sauvagesia* the cuticle is furnished with small knobs. A finely granular coating of wax on the surface of the leaf is stated by Reiche to occur in *Viola Philippii*, Leyb. and *V. atropurpurea*, Leyb. According to Diels, a many-layered **hypoderm** is present in *Hymenanthera latifolia*.

The **stomata** with their subsidiary cells belong either to the Cruciferous or to the Rubiaceous type. According to Vesque, the first type is found in many species of *Viola*, in *Ionidium thesiifolium*, DC., in certain species of *Alsodeia* (*A. castaneaefolia*, Spreng., *A. guianensis*, Eichl.), in *Paypayrola longifolia*, Tul. and *Leonia cymosa*, Mart.; this type becomes indistinct or occurs side by side

[1] See especially the synopsis in Kraemer's work, pp. 26, 27; the mucilaginous inner walls are, however, erroneously spoken of by Kraemer as mucilage-cells.

with a different arrangement of the neighbouring cells in *Alsodeia Roxburghii*, 'Wall.' and *A. ulmifolia*, 'Kth.,' in *Amphirrhox longifolia*, Spreng., *Hymenanthera Banksii*, F. v. M. and in *Sauvagesia*. *Anchietea salutaris*, St. Hil., '*Corynostylis frangulaefolia*, H. B. K.,' *Noisettia longifolia*, St. Hil., *Isodendrion pyrifolium*, A. Gr., *Melicytus ramiflorus*, Forst., and *Sauvagesia erecta*, L. have two subsidiary cells placed parallel to the pore (Rubiaceous type), while in *Ionidium suffruticosum*, Ging. and *I. lineare*, Torr., as well as in *Viola alpestris*, Jord., transitions from the Cruciferous to the Rubiaceous types are present. The position of the stomata varies. They are either deeply sunk, or they lie in the plane of the epidermis of the leaf. They are either present only on the lower side of the leaf, or on both sides. According to Reiche, *Viola tridentata*, Menz. and *V. muscoides*, Philippi are extremely noteworthy in this respect, as in these species the stomata are found only on the upper side of the leaf.

The small **veins** are mostly embedded in the mesophyll; sometimes colourless parenchyma or collenchyma adjoins them above and below. Sclerenchyma is wanting in the veins of the herbaceous species and of a large number of woody species. In numerous woody Violarieae (*Alsodeia castaneaefolia, Paypayrola longifolia, Melicytus ramiflorus*, &c.) the vascular bundles of the veins are accompanied above and below by a well-developed sclerenchyma-strand or are surrounded by a ring of sclerenchyma. The midrib of the smaller leaves contains only one vascular bundle; in larger leaves the vascular system of the midrib consists of two bundles, of which the upper one is inversely orientated with respect to its xylem and phloem. A still more complicated structure of the vascular system is found in the midribs of large leaves. Vesque makes some special statements on this subject and also on the arrangement of the vascular bundles in the petiole; I only refer to these briefly here, because they are of importance for specific diagnosis only.

We owe a recent, detailed investigation on the occurrence of **crystals** in the Violarieae to Borodin; according to this work clustered crystals as well as solitary oblique (clinorhombic) crystals are present in the mesophyll, but in no case in the epidermis. With regard to the occurrence or absence of these crystalline elements and their distribution in the leaf-tissue Borodin distinguishes the following eight cases, which are in part characteristic of certain genera:

(1) *Lavradia*-type: crystals are absent; to this type belong all four species of *Lavradia*, the single investigated species of *Paypayrola*, two of *Sauvagesia*, and two of *Viola*.

(2) *Viola*-type: scattered cells containing clustered crystals in the mesophyll; crystals absent along the veins. Fifty-nine species of *Viola* and six of *Ionidium*.

(3) *Sauvagesia*-type: cells containing clustered crystals exclusively along the veins. Four species of *Sauvagesia* and one of *Ionidium*.

(4) Combination of the two preceding types: four species of *Sauvagesia* and one of *Ionidium*.

(5) *Ionidium*-type: solitary oblique (clinorhombic) crystals exclusively along the veins. Twenty-five species of *Ionidium*, three of *Alsodeia* as well as species of other small genera.

(6) Solitary clinorhombic crystals along the veins as well as scattered in the mesophyll. Two species of *Ionidium*, two of *Alsodeia*, and three representatives of smaller genera.

(7) *Alsodeia*-type: oblique (clinorhombic) crystals along the veins; clustered crystals scattered in the mesophyll. Twenty-two species of *Alsodeia*; five of *Hymenanthera*, four of *Ionidium*, all three of *Agation*, both species of *Corynostylis* and one of *Schweiggeria*.

(8) *Amphirrox*-type: just as in 7, clustered crystals, however, not scattered in the mesophyll, but strictly above the veins. All three species of *Amphirrox* and one of *Hybanthus*.

Inulin has hitherto only been met with in the root of *Ionidium Ipecacuanha*, St. Hil. (see Flückiger, Pharmakogn., 2nd Edit., p. 396).

Regarding the **hairy covering** it must be pointed out, that only simple, unicellular or uniseriate trichomes occur in the Order. True glandular hairs have not been observed, but only glandular shaggy hairs on the leaf-teeth of species of *Viola* and other Violarieae, e.g. *Lavradia glandulosa*, St. Hil. These latter have been investigated by Hanstein in *Viola*, where they are composed of a multiseriate nucleus of elongated cells, which is enclosed by a mucilage-secreting epidermis resembling palisade-tissue in form [1].

3. Structure of the Axis. Little is known as to the structure of the **wood** [2] of the woody genera and still less (from the researches of Harms and Gilg) as to the structure of the cortex. The medullary rays of the wood are of varied breadth; many very broad medullary rays, which traverse the xylem longitudinally for a considerable distance and thereby cause an approximation to the *Aristolochia*-type, are found in *Anchietea salutaris*, St. Hil. (H. Schenck). The size of the lumina of the vessels varies (maximum-diameter ·018 mm. in *Schweiggeria floribunda*, St. Hil. and ·082 mm. in *Anchietea pyrifolia*, St. Hil.), as also does the arrangement of the vessels. The vessels sometimes (*Paypayrola*) bear scalariform bordered pits on the walls by which they touch one another; when in contact with medullary-ray-parenchyma they bear simple pits side by side with bordered pits as well as intermediate forms. The perforations of the vessels are either (1) exclusively scalariform (species of *Paypayrola*, *Amphirrhox*, *Gloeospermum*, *Alsodeia*, and *Leonia*), or (2) both simple and scalariform (species of *Corynostylis*, *Noisettia*, *Ionidium*, *Schweiggeria*, *Anchietea*, *Alsodeia*, *Hymenanthera*, *Lavradia* and *Sauvagesia*), in which case the scalariform perforations usually have few bars or are developed as distorted forms, or (3) exclusively simple (*Melicytus ramiflorus*, Benth. according to Harms). The wood-parenchyma is little developed. The wood-prosenchyma is in general simply-pitted. Septation of the lumen and occurrence of a gelatinous layer are not rare in the wood-prosenchyma. In *Anchietea* and *Corynostylis* wood-prosenchyma with bordered pits has been observed accompanying that with simple pits.

Harms describes groups of bast-fibres in the pericycle for the **cortex** of species of the genera *Alsodeia*, *Amphirrhox*, *Melicytus* and *Paypayrola*, these groups being united by stone-cells into a completely, or almost completely, closed mechanical ring. According to Gilg, the genera of Sauvagesieae (*Neckera* has not yet been investigated) quite generally possess cortical vascular bundles, and are for this reason united with the Ochnaceae by Gilg in accordance with Engler. These cortical bundles are represented in a specially marked manner in *Schuurmansia* and *Lavradia*, less distinctly and in small numbers in *Sauvagesia* and *Leitgebia*. Moreover Gilg states that in all the Sauvagesieae mucilage-sacs or (lysigenous ?) mucilage-passages are developed in the cortex, and often also in the pith, being especially well-marked in *Schuurmansia Henningsii*, K. Schum.

Literature: Hanstein, Harz- u. Schleimabs., Bot. Zeit. 1868, p. 751 and Tab. xi.—Reinke, Sekretionsorg., Pringsheim Jahrb., Bd. x, 1876, pp. 169, 170 and Taf. xii.—De Bary, Vergl. Anat., 1877.—Vesque, Nouv. Arch. Mus. d'hist. nat., sér. 2, t. v, 1882–3, pp. 320–32 and pl. 20.—Blenk, Flora 1884, p. 106 and separate copy, p. 20.—Solereder, Holzstruktur, 1885, pp. 64–6.—Radlkofer, Sitz-Ber.

[1] Myrosin-cells are not present in the Violarieae (see Guignard, Journ. de Bot., t. vii, 1893, p. 455 et seq.), not even in the seed, where Spatzier (Pringsheim Jahrb., Bd. xxv, 1893, p. 71) incorrectly states that they occur.

[2] The genera, species of which have been investigated with regard to the structure of their wood, are enumerated in the description of the perforations of the vessels.

Münch. Akad. 1890, p. 186.—Borodin, Arb. St. Petersb. naturf. Gesellsch. 1891, pp. 177–205, Russian; abstract by Rothert in Bot. Centralbl. 1892, ii, p. 51.—Benecke, Nebenz. d. Spaltöffn., Bot. Zeit. 1892, p. 574.—Gilg, in Natürl. Pflanzenfam., iii. Teil, Abt. 6, 1893, p. 134.—Harms, Engler, Bot. Jahrb., Bd. xv, 1893, pp. 622, 623.—Reiche, *Violae* chilenses, Engler, Bot. Jahrb., Bd. xvi, 1893, pp. 409–11 and Taf. vi.—H. Schenck, Anat. d. Lianen, 1893, pp. 71, 72.—Reiche u. Taubert, in Natürl. Pflanzenfam., iii. Teil, Abt. 6, 1895, pp. 324, 325.—Diels, Veg.-Biol. v. Neuseeland, Engler, Bot. Jahrb., Bd. xxii, 1896, pp. 230 and 249.—Parmentier, Ann. sc. nat., sér. 8, t. ii, 1896, p. 3 et seq.—Kraemer, *Viola tricolor*, L. etc., Diss., Marburg, 1897, 67 pp. and 5 Tab.

CANELLACEAE.

1. Review of the Anatomical Features. The Canellaceae have a series of characteristic features in common, by means of which any species can be easily recognized as a member of the Order. These features are the following: the occurrence of secretory cells in the parenchymatous tissues of axis and leaf; the absence of glandular hairs; the excretion of oxalate of lime in the form of clustered and solitary crystals; the possession of narrow medullary rays, which are broadened outwards in the cortex; vessels with a small lumen, with scalariform perforations having many bars and with bordered pits even when in contact with medullary-ray-parenchyma; wood-prosenchyma with bordered pits; the origin of a periderm with large lumina and thin walls immediately below the epidermis of the branch; the development of a characteristic phelloderm consisting of cells with their membranes sclerosed on one side only; and the absence of a ring of sclerenchyma in the pericycle. The stomata belong to the Rubiaceous type; side by side with the stomatal apparatus of this type, however, there sometimes (*Cinnamosma*) also occur other types, in which the stomata are surrounded by several irregularly placed epidermal cells. Trichomes have not been observed.

The anatomical structure of the Canellaceae (especially as concerns the secretory cells and the nature of the wood-vessels and the wood-prosenchyma) points to close affinity with the Magnoliaceae (Wintereae).

2. Structure of the Leaf. The mesophyll is bifacial in structure. The **epidermal cells** have straight lateral walls; according to Vesque, marginal pits are present in *Cinnamosma fragrans*, Baill. In the same species a one-layered **hypoderm** is found below the epidermis on the upper side of the leaf. The **stomata**, which occur only on the lower side of the leaf, are, in *Canella alba*, Murr., provided with one subsidiary cell on each side parallel with the pore; in *Cinnamosma fragrans* other stomata also occur, which are irregularly surrounded by several epidermal cells. The vascular bundles of the smaller **veins** are embedded in the mesophyll; they are accompanied above and below by strands of bast-fibres. The midrib of the leaf contains one band-shaped vascular bundle, which is likewise provided with a band of sclerenchyma both above and below. The **petiole** encloses three vascular bundles which are accompanied by sclerenchyma in *Cinnamosma* (but not in *Canella*).

Specially noteworthy is the occurrence of roundish or lenticular **secretory cells**, with yellow contents easily soluble in spirit and an (always ?) suberized cell-wall. These occur in the leaf-tissue in all the three genera (*Canella, Cinnamosma, Cinnamodendron*), causing transparent dots when the leaf is cut open; they have also been observed in the pith and cortex of the axis in *Canella* and *Cinnamodendron*.

Oxalate of lime is usually excreted in the form of clustered crystals in the leaf and axis. Small octahedral solitary crystals are stated by Vesque to occur in the lower epidermis of the leaf of *Canella alba*; solitary crystals of the usual size and shape are found in the parenchyma of the medullary rays in *Canella* and *Cinnamodendron*.

3. Structure of the Axis. The **wood** of the Canellaceae, according to an examination of *Canella alba*, Murr. and *Cinnamodendron axillare*, Endl., contains 1–2- rarely 3-seriate medullary rays, isolated vessels with roundish lumen and of a maximum diameter of ·044–·066 mm., little wood-parenchyma and wood-prosenchyma with typical bordered pits. The end-walls of the vessels are strongly inclined and have scalariform perforations; the perforation sometimes also consists of a considerable number of circular holes (*Canella alba*). The wall of the vessel bears bordered pits even in contact with medullary-ray-parenchyma.

The structure of the **cortex** has been investigated by Möller in the genera *Cinnamodendron* and *Canella*. According to him the periderm arises early immediately below the epidermis, and consists of cork-cells with large cavities and thin walls. On the inner side of the periderm and separated from it by the cork-cambium, there occurs in the cortex of the older branches a fairly thick layer of phelloderm-tissue, consisting of cells which have their inner tangential walls strongly thickened in the form of a U and pitted, and often show the same radial arrangement as the cork-cells. The primary cortex and the bast contain secretory cells, which in *Cinnamodendron* remain thin-walled, but thicken their walls in *Canella*. The medullary rays of the cortex become considerably broader towards the outside in both genera. The sieve-tubes in both genera have scalariform sieve-plates. In *Canella* sclerenchyma is wanting in both primary and secondary cortex; in *Cinnamodendron* bast-fibres and sclerenchyma-cells resembling rod-cells are present in the secondary cortex.

Literature: De Bary, Vergl. Anat., 1877, p. 152 et seq.—Zacharias, Bot. Zeit. 1879, p. 627.—Möller, Rindenanat., 1882, pp. 252–4.—Vesque, Nouv. Arch. Mus. d'hist. nat., sér. 2, t. v, 1882–3, pp. 332–5.—Blenk, Flora 1884, p. 106 and separate copy, pp. 20, 21.—Solereder, Holzstr., 1885, p. 66.—Parmentier, Assoc. franç., Caen 1894, 2e partie, p. 623.—Warburg, Natürl. Pflanzenfam., iii. Teil, Abt. 6, 1895, p. 315.—Parmentier, Bull. scient. de la France et de la Belgique, 1896.

BIXINEAE.

1. Review of the Anatomical Features. Anatomical characters common to all members are almost entirely wanting in the Order. The structure of the wood shows fair uniformity in so far as (1) the wood-prosenchyma never possesses large, distinct bordered pits on its walls, but only pits with small, often indistinct border, or simple pits, and (2) the wood-prosenchyma is frequently septate by means of delicate division-walls. The perforations of the vessels on the other hand, vary; they are either exclusively simple, or exclusively scalariform, or simple and scalariform in the same species; the remaining structural features of the wood vary in like manner. In the pericycle either isolated groups of bast-fibres are present (*Azara, Dasylepis, Dendrostylis, Grandidiera, Gynocardia*, and *Oncoba*), or a composite and continuous sclerenchymatous ring (*Hydnocarpus. Ryania, Taraktogenos*); in certain cases, secondary hard bast also occurs; the cork originates subepidermally in the few cases investigated. The stomatal apparatus belongs to the Rubiaceous or to the Cruciferous type. Oxalate of lime occurs in the form of clustered and ordinary solitary crystals. The occurrence of small groups of crystal-bearing epidermal cells in the leaf of certain species of *Laetia, Ludia, Oncoba, Poggea, Scolopia*, and *Xylosma* is very noteworthy. In addition to mucilaginous epidermal cells in the leaf (in *Aphloia* and *Cochlospermum*), secretory cells, which in part are elongated, tubular, and branched, occur in the genera *Amoreuxia, Bixa, Cochlospermum*, and *Xymalos*; schizogenous secretory cavities occur in *Laetia*, and (apparently lysigenous) mucilage-passages in *Amoreuxia, Bixa, Cochlospermum* and *Sphaero-*

sepalum; the secretory cells and cavities cause transparent dots or fine striae in the leaf. The hairy covering consists of clothing and glandular hairs. The clothing hairs are either simple unicellular or uniseriate trichomes or unicellular bracket-hairs (*Poggea*) or tufted hairs (*Bixa, Kiggelaria,* and *Ryania*) or peltate hairs (*Bixa* and *Mayna*). The glandular hairs are short- or long-stalked, and have a disc-shaped head divided exclusively by vertical walls (*Oncoba, Poggea*). Lastly, of special anatomical features of the leaf, which may be made use of for specific diagnosis, the following should be mentioned: development of hypoderm (in species of *Erythrospermum, Kiggelaria, Laetia, Ludia,* and *Xylosma*); papillose nature of the lower epidermis (*Idesia polycarpa*, Maxim.); and the occurrence of spicular cells in the mesophyll (species of *Ryania*).

2. STRUCTURE OF THE LEAF[1]. The **mesophyll** is, as a rule, bifacial in structure; in the thick leaves of *Xylosma ellipticum*, Tul., it consists entirely of palisade-tissue. In certain species of *Ryania* (' *R. dentata*, H. B. K. and *R. Schomburgkii*, Klotzsch ') the mesophyll is, according to Harms, traversed by ' simple and branched spicular cells, running irregularly in the leaf.' The **epidermal cells** have straight or undulated lateral walls. The cuticle is smooth, striate or granular; a layer of wax is found in *Oncoba glauca* and *Laetia lucida*, Tul. Not uncommonly the inner membranes of the epidermal cells are mucilaginous, as Vesque and Blenk mention for *Cochlospermum* and *Aphloia*. According to Vesque in *Eriudaphus* (*Scolopia*) *Mundtii* the epidermal cells are divided by walls parallel to the surface of the leaf, and the lower daughter-cells, thus produced, are frequently divided by a small number of vertical walls; similar tangential divisions also occur in the epidermis of the leaf of *Cochlospermum Gossypium*, DC. Hypoderm, according to Vesque, is present on the upper side of the leaf of *Xylosma infestum*, Griseb., *Ludia sessiliflora*, Lam., *Kiggelaria Dregeana*, and *Erythrospermum laxiflorum*; it is two-layered in the last-named species, and one-layered elsewhere; according to my own observation hypoderm likewise occurs in *Laetia apetala*, Jacq., and is there 1–2-layered. Further, in a large number of species a differentiation of the epidermis occurs, in so far as among the ordinary epidermal cells there are intercalated single epidermal cells or groups of 2–4 small roundish epidermal cells, which contain clustered crystals. Even though these small crystal-idioblasts, in accordance with the researches of Vesque, are in general only of specific value, they may in certain cases be of great value for the recognition of sterile material of Bixineae. These crystal-idioblasts have been observed by Vesque in species of *Oncoba* (*O. glauca*), *Laetia* (*L. lucida*, Tul., and likewise *L. apetala*, Jacq. according to my own observation), *Ludia* (*L. myrtifolia*, Lam.), *Scolopia* (*Eriudaphus Mundtii*), and *Xylosma* (*X. ciliatifolium*, Eichl., *X. ellipticum*, Tul. and *X. infestum*, Griseb.), by me also in *Poggea alata*, Gürke. Radlkofer describes a papillosely differentiated epidermis on the lower side of the leaf of *Idesia polycarpa*, Maxim. The **stomata** have hitherto only been observed on the lower side of the leaves. According to their development the stomata belong to the Cruciferous or Rubiaceous type. In the majority of the genera (*Pangium, Xylosma, Flacourtia, Scolopia, Laetia, Ludia, Mayna, Oncoba*) in the mature condition, one subsidiary cell is placed on each side of the guard-cells parallel with the pore; transitions to the Cruciferous type are seen in *Kiggelaria, Hydnocarpus, Dendrostylis,* and *Erythrospermum*, while in *Aphloia madagascariensis* the pronounced Cruciferous type is present.

The vascular bundles of the smaller **veins** are as a rule accompanied above and below by a strand of sclerenchyma, which not uncommonly reaches nearly as far as the upper and lower epidermis. In *Aphloia madagascariensis* the

[1] Most important literature: Vesque and Blenk, loc. cit.

sclerenchyma is completely absent. The median vein almost always consists of an arc-shaped vascular bundle with sclerenchyma, rarely (*Cochlospermum*) without sclerenchyma. In the midribs of the larger leaves of *Erythrospermum laxiflorum* the fibro-vascular system almost forms a ring, because in addition to the arc-shaped vascular bundle there is a second one with inverse orientation. Lastly, the midrib of the leaf of *Bixa Orellana* shows a ring of vascular bundles without sclerenchyma, enclosing a band of vascular bundles, the xylem of which is directed downwards. The **petiole** also shows similar variety; with regard to its structure, only the examples cited by Vesque need be referred to here.

Oxalate of lime is present in the form of oblique (clinorhombic) solitary crystals or of clustered crystals.

Internal **secretory organs**[1] occur in the Bixineae (apart from the mucilaginous epidermal cells already described) in three forms, namely, as secretory cells, secretory cavities, and mucilage-canals. Secretory cells are found in *Amoreuxia*, *Bixa*, *Cochlospermum*, and *Xymalos*, secretory cavities in *Laetia*, mucilage-canals in *Amoreuxia*, *Bixa*, and *Cochlospermum*, as well as in the genus *Sphaerosepalum*, Bak., removed by Warburg from the Guttiferae to the Bixineae.

According to my own observations, the **secretory cells** of *Amoreuxia Wrightii*, A. Gray are large, tubular cells of the mesophyll, which are frequently branched and are filled with yellowish or reddish contents; they are visible even with the naked eye as small transparent striae. Quite similar secretory cells, which in like manner are observable with the naked eye or with a lens, occur in the species of *Cochlospermum* investigated by Blenk (*C. Gossypium*, DC., *C. insigne*, St. Hil., *C. orinoccense*, Steud., and *C. serratifolium*, DC.); in these the contents in the dried leaf are sometimes formed of polygonal grains of lemon-yellow colour. In *Cochlospermum niloticum*, 'Schweinf.' the secretory cells in question have also been observed in the pith and cortex of the branch (Harms). According to Blenk the secretory cells of *Bixa Orellana*, L. have wide lumina, are filled with a yellow or brown brittle resin, and in outline are frequently oblong and lobed; they occur in the mesophyll, and likewise cause pellucid dots. Van Tieghem has met with the secretory cells of *Bixa Orellana* in the primary cortex and bast of the branch, as well as in the root. Lastly, the secretory cells observed by Harms in *Xymalos monospora*, Baill. are relatively small and only produce delicate transparent dots. It should be noted with regard to the above-mentioned secretory cavities of *Laetia*, that they were wrongly described by Blenk as secretory cells, as has already been correctly pointed out by Warburg; according to my examination of *Laetia apetala*, Jacq., they possess a distinct one-layered epithelium, and have consequently probably arisen in a schizogenous manner. Besides those in *L. apetala*, Jacq., secretory cavities have been observed in *L. corymbulosa*, Spruce, *L. suaveolens*, Benth., and *L. Thamnia*, Sw. The mucilage-canals are apparently of lysigenous origin. They are found in the branch both at the periphery of the pith (in *Cochlospermum Gossypium*, *C. insigne*, and *C. orinoccense*, as well as in *Bixa Orellana* according to my own observation; in *Cochlospermum hibiscoides* and *Amoreuxia palmatifida*, according to Harms), and also in the cortex (in *Cochlospermum Gossypium*, according to Van Tieghem, in *Amoreuxia palmatifida*, *Bixa Orellana* and *Cochlospermum hibiscoides* according to Harms).

Lastly, with regard to the **hairy covering**, simple unicellular hairs are not uncommon. In *Poggea alata*, Gürke, I have occasionally met with simple uniseriate trichomes, which are thick-walled and septate by means of delicate cross-walls, and, in addition to these, hairs which are curved at the tip like a hook (bracket-hairs). Further, in this Order tufted hairs occur, which consist of a few unicellular component hairs sunk side by side in the epidermis (*Bixa*,

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[1] The statements of Vesque as to the secretory organs of the Bixineae are inaccurately presented and could therefore not be taken into consideration in the following description without a thorough reinvestigation on my part.

Kiggelaria, Ryania). Lastly, *Bixa Orellana* and *Mayna laurina* are distinguished by the possession of peltate hairs; the latter have a longer or shorter stalk, consisting of a few cells or a few rows of cells, and a shield, which has an entire margin and is irregularly many-celled, the cells being polygonal in surface view. Glandular hairs have been observed by me in *Poggea alata* and *Oncoba Welwitschii*, Oliv.; their disc-shaped head is divided exclusively by vertical walls into four or more radially situated cells.

3. STRUCTURE OF THE AXIS [1]. Our knowledge of the structure of the axis in this Order is restricted almost solely to the structure of the wood. The statements of Turner as to the nature of the cortex are incomplete and in part not clearly presented, so that they can only be shortly noticed here; the statements of Harms are also incomplete in this respect.

The breadth of the medullary rays in the wood, the arrangement of the vessels and the lumina of the vessels (maximum diameter, ·036–·093 mm.) are variable and present no common characters. On the vessel-wall, where it is in contact with the parenchyma of the medullary rays, one-sided bordered pits occur (*Bixa, Aberia, Flacourtia*), or transitions from these to simple pits (*Carpotroche, Cochlospermum, Oncoba*), sometimes large simple pits (*Kiggelaria*). The perforations of the vessels are in part exclusively simple, in part exclusively scalariform with many bars, in part scalariform and simple; in this third case the scalariform perforation of the vessels may be restricted to the neighbourhood of the primary wood or may occur in the secondary wood also.

The following more detailed statements are derived from my own investigations and from those of Harms and Turner. The following plants have exclusively simple perforations: *Amoreuxia palmatifida, Bixa Orellana*, L., *Cochlospermum insigne*, St. Hil., *C. hibiscoides, Flacourtia sapida*, Roxb. according to Turner (? D. V.), *Laetia Thamnia*, Sw. according to Turner (? D. V.). The perforations of the vessels are mostly simple, while scalariform perforations with 5–8 bars are present in the neighbourhood of the primary wood only in: *Carpotroche brasiliensis*, Endl., *Grandidiera Boivini*, Jaub., *Oncoba spinosa, Ryania Schomburgkii*, Klotzsch, *Trimeria* sp. In addition to simple perforations, scalariform openings, which usually have few (2–10) bars, are present in the secondary wood also in: *Aberia verrucosa*, Hochst., *Azara microphylla*, Hook., *A. dentata*, R. et P., *A. alpina*, Poepp. et Endl., *A. salicifolia*, Gr., *Dendrostylis* sp., *Dovyalis* sp., *Flacourtia obtusa*, Hochst., *Gynocardia* sp., *Kiggelaria africana*, L., *Pangium edule*, Reinw. Lastly, exclusively scalariform perforations of the vessels, mostly with numerous bars, occur in: *Azara Fernandesiana*, Gay, *A. serrata*, R. et P., *A. lanceolata*, Hook., *A. umbellata*, Phil., *Dasylepis racemosa*, Oliv., *Erythrospermum tinifolium*, Sieb., *Hydnocarpus Wightiana*, Bl., *Taraktogenos* sp., *Xymalos monospora*, Baill. From the above statements it results, that for the members of the tribe Bixeae exclusively simple perforation of the vessels appears to be characteristic, for the remaining tribes a tendency to the formation of scalariform perforations (that is the subordinate occurrence of the latter side by side with simple openings), or, on the other hand, the exclusive occurrence of scalariform perforations.

Spiral thickening of the walls of the vessels has been observed in *Hisingera japonica* and in the above-cited species of *Azara* with scalariform and simple perforation of the vessels; spiral striation has been observed in *Ryania Schomburgkii*, Klotzsch. The wood-parenchyma is fairly abundantly developed in *Bixa*, elsewhere it is subordinate in amount. The wood-prosenchyma varies in character, but never exhibits large bordered pits on its walls. The pits of the wood-prosenchyma of *Bixa* show a fairly distinct and rather large border; in the other genera investigated by me (*Aberia, Carpotroche, Cochlospermum, Flacourtia, Kiggelaria* and *Oncoba*) the border is either smaller and in that case frequently indistinct, or it is completely absent. I observed division-walls in

[1] See especially Solereder and Turner, loc. cit.

the wood-prosenchyma of *Aberia*, *Carpotroche*, *Flacourtia*, *Kiggelaria*, and *Oncoba*; Turner states that the same feature occurs in the species of *Aberia*, *Azara*, *Bixa*, *Carpotroche*, *Flacourtia*, *Gynocardia*, *Hisingera*, *Hydnocarpus*, *Idesia*, *Kiggelaria*, *Laetia*, *Scolopia* and *Xylosma*. Now and then the wood-prosenchyma-cells are specially strongly thickened, owing to the occurrence of a gelatinous membrane.

The following facts are known as to the structure of the **cortex**. According to Harms, either isolated groups of bast-fibres or a composite and continuous sclerenchymatous ring (cf. the general diagnosis) are found in the pericycle, In the secondary bast bands of bast-fibres are sometimes present, according to Turner; in *Bixa* and *Cochlospermum*, according to Van Tieghem, a stratification of the bast into hard and soft bast, similar to that in the Malvaceae, &c., occurs. The cork arises immediately below the epidermis in *Idesia polycarpa* (according to J. E. Weiss) and in *Azara Gilliesii* and *Kiggelaria africana* (according to Douliot); in the two species last named, a phelloderm identical with that in the Cannellaceae (q.v.) is also differentiated.

Literature: Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 74 and 370.—Vesque, Nouv. Arch. Mus. d'hist. nat., sér. 2, t. v, 1882–3, pp. 335–45 and pl. 20, 21.—Blenk, Flora 1884, p. 107 et seq., separate copy, pp. 21–4.—Turner, Vergl. Anatomie der B. etc., Diss., Göttingen, 1885—Solereder, Holzstr., 1885, pp. 66–8.—Van Tieghem, Ann. sc. nat., sér. 7, t. i, 1885, pp. 79, 80.—Bachmann, Schild., Flora 1886, separate copy, p. 31.—Douliot, Ann. sc. nat., sér. 7, t. x, 1889, p. 343.—Radlkofer, Sitz.-Ber. Münch. Akad. 1890, p. 251.—J. E. Weiss, Denkschr. Regensb. bot. Gesellsch. 1890, separate copy, p. 67.—Harms, Engler, Bot. Jahrb., Bd. xv, 1893, pp. 612–18.—Warburg, in Natürl. Pflanzenfam., iii. Teil, Abt. 6 a, 1893, pp. 3, 4 and iii. Teil, Abt. 6, 1895, p. 308.—Briquet, Hydathodes fol. des *Scolopia*, Bull. Herbier Boissier 1898, pp. 503, 504.

PITTOSPOREAE.

1. Review of the Anatomical Features. The following anatomical features are characteristic of the Order as a whole[1]: the occurrence of schizogenous resin-canals in the pericycle (in thick stems in the secondary bast also, but never in the pith or primary cortex; in the roots opposite the xylem and phloem-groups of the vascular system, with which the appearance of double the usual number of lateral rootlets is connected); the stomata with their subsidiary cells parallel to the pore; the spirally thickened, pitted vessels of the wood with their simple perforations and with bordered pits, even where in contact with the parenchyma of the medullary rays; the lack, or at least the scanty development of sclerenchyma and the tendency of the tissues, and especially of the bast, to become collenchymatous. Oxalate of lime is present in the form of clustered crystals, ordinary solitary crystals and styloids (the last only in the bast). The hairy covering is formed by simple, uniseriate trichomes, with two or three short basal cells and a long end-cell, by two-armed hairs with a few-celled stalk, and by club-shaped few-celled glandular hairs. Gelatinization of the epidermis of the leaf has not been observed in any member of the Order; on the other hand, in the leaves of certain species a hypoderm or a doubling of the epidermis is found. The place of origin of the periderm varies.

2. Structure of the Leaf[2]. The structure of the leaf is either centric (*Pittosporum phillyraeoides*, DC., *Bursaria spinosa*, Cav., &c.), or bifacial. The epidermal cells, especially those on the upper side of the leaf, frequently

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[1] With the exception of the genus *Chalepoa*, which according to Van Tieghem must be removed from the Pittosporeae on account of the absence of resin-canals, and in agreement with this has quite recently been transferred to the Saxifragaceae by Pax and Engler.

[2] According to Vesque, Nouv. Arch. du Mus. d'hist. nat., loc. cit., and a manuscript of Dr. H. Grote dealing with the anatomy of the leaf and axis of the Pittosporeae.

possess strongly thickened outer walls; the latter sometimes (*Pittosporum phillyraeoides*, DC.) exceed the height of the epidermal cells in thickness. The lateral walls of the epidermal cells are mostly straight, less frequently they are more or less strongly undulated. In *Marianthus tenuis*, Benth., the epidermal cells of the upper side of the leaf are produced into conical papillae. A doubling of the epidermis occurs in many species of *Pittosporum* in consequence of the appearance of division-walls, which are parallel to the surface of the leaf; such division-walls are either present locally, e.g. in *Pittosporum pachylobum*, Tul., *P. reflexum*, Cunn., *P. tetraspermum*, W. et A., *P. Tobira*, Ait., *P. undulatum*, 'Lam.' and *P. zeylanicum*, Wight, or generally, i.e. in all the epidermal cells, e.g. in *Pittosporum carnifolium*, Cunn., *P. coriaceum*, Ait. and *P. Kirkii*, Hook. f. In both cases the cells of the lower layer usually correspond entirely with those of the upper. Exceptions to this, however, also occur, e.g. in *Pittosporum carnifolium*, in which the lower layer consists of larger cells than the upper, this being due to secondary division in the upper layer of epidermal cells after the lower layer of cells has been divided off. The upper side of the leaf of *Pittosporum phillyraeoides* has an extremely remarkable two-layered epidermis. In this species the upper layer consists of the usual low tabular cells, while, on the other hand, the lower layer, which has been split off from the upper by horizontal division, consists of much-elongated, palisade-like cells with their side-walls minutely folded. The cuticle is either smooth, or variously marked, e.g. punctate or striate. The **stomata** are accompanied by two or by several subsidiary cells, which are parallel to the pore, and are mostly also distinguished by their thinner walls from the other epidermal cells. Dr. Grote, according to his manuscript, has observed this type of stoma in all the nine genera of the Order, so that it represents an excellent ordinal character. The stomata lie in the plane of the other epidermal cells or are sunk in the epidermis.

The vascular bundles of the small **veins** of the leaf are usually embedded in the mesophyll; sometimes, however, they are connected with the upper epidermis by means of colourless, collenchymatous tissue. The **petiole** contains 3, 5, 7 or more vascular bundles, arranged in the form of an arc, or rarely (viz. in small leaves) a single bundle. The absence or rare occurrence of sclerenchyma accompanying the vascular bundles is worthy of note. It is replaced by collenchyma, which is mainly present in the ground-tissue of the midrib and petiole; but other tissues also have a tendency to become collenchymatous, especially the soft bast, which will be more fully discussed in the description of the axis.

Oxalate of lime is excreted in three forms in the Pittosporeae: in the form of clustered crystals, ordinary solitary crystals and columnar crystals (called styloids). While the first two forms occur abundantly in the mesophyll, where they are frequently contained in specially large crystal-sacs (*Marianthus tenuis*, *Sollya heterophylla*, *Cheiranthera linearis*, *Pittosporum* sp., &c.), further, in the ground-tissue of the veins and of the petiole, and in the pith and primary cortex of the axis, the styloids are restricted to the bast of the axis, but, as it appears, are to be found there in all members of the Order.

Schizogenous **secretory canals** are present in all the genera (excluding *Chalepoa*, see above). They are found in the axis, in the root and in the leaf, and in *Pittosporum Tobira*, according to Dr. Grote, they can also be demonstrated in the sepals and petals, as well as in the ovary, but not in the stamens. But not only is the occurrence of these secretory canals (which have colourless, yellow or reddish, resin-like contents) characteristic of the Order, but also their position, for they are invariably found in the pericycle in all the organs named above. The secretory canals never occur in the pith and primary cortex of stem and

root, nor are they found in the ground-tissue of the leaf. On the other hand, the occurrence of secretory canals in concentric layers has been observed in the secondary bast of branches of sufficient thickness in species of *Pittosporum*. In young roots of *Pittosporum*, *Sollya*, and *Citriobatus*, where the fibro-vascular system, according to Van Tieghem, usually consists of 5, 6, or 7 radial vascular bundles, which enclose a pith, the secretory canals are found on the outer side not only of the phloem-groups, but also of the xylem-groups. As a consequence, in the genera named and probably also in the remainder of the Pittosporeae, the lateral roots cannot develop, as they ordinarily do, on the outer side of the xylem-groups and in corresponding number; here, the number formed is double that of the xylem-strands, one occurring in each case between the secretory passage opposite a xylem-group and the neighbouring secretory passage opposite a phloem-group. This peculiarity is also found in the Araliaceae and Umbelliferae (q.v.) and is made use of by Van Tieghem in support of genetic relationship between these Orders and the Pittosporeae. The secretory canals in question were demonstrated by Van Tieghem in the leaf and in the axis of *Pittosporum*, *Hymenosporum*

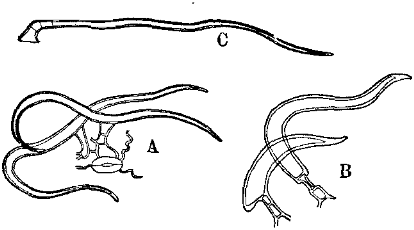

FIG. 22. A, Two-armed hair of *Pittosporum bicolor*. B, One-armed trichome on a young branch of *P. coriaceum*. C, Uniseriate hair on a young branch of *Marianthus tenuis*.—After Vesque.

(1 species examined), *Ixiosporum* (1), *Citriobatus* (1), *Bursaria* (1), *Marianthus* (1), *Cheiranthera* (1), *Pronaya* (1), *Sollya* (2), *Billardiera* (2); Grote investigated a far larger number of species (above 50 in all) of the genera cited, and met with the secretory canals throughout and always in the same position.

In most members of the Order a more or less strongly developed **hairy covering** is present, which is constituted, according to Vesque, by three different forms of hairs, which in part, however, exhibit transitions. Firstly, there occur uniseriate, few-celled hairs with two or three very short basal cells and a long pointed end-cell; the cells, as a rule, have thick walls and narrow lumina (*Billardiera*, *Marianthus*, Fig. 22, *C*, *Pronaya*, *Sollya*). The second form is represented by two-armed hairs (Fig. 22, *A*). These have a short, few-celled stalk, the cells of which are strongly thickened; the two-armed terminal cell is either thin-walled or thickened, being deciduous in the former case (*Bursaria*, *Citriobatus*, *Pittosporum*). The two-armed hairs are connected with the first described form of hair by transitions (Fig. 22, *B*). Thirdly, club-shaped glandular hairs (*Hymenosporum*) occur, which are similar in structure to those of *Helianthemum*, consisting of a row of cells, which is somewhat curved at its end. According to Grote's communication, glandular hairs of this kind occur not only in *Hymenosporum*, but also in species of *Pittosporum* (e.g. *P. coriaceum*, Ait., and *P. umbellatum*, Gaertn.), and of *Bursaria* (*B. incana*, Lindl.).

According to Grote's investigations, generic value is not, as a rule, to be attributed to the different forms of hairs in this Order.

3. STRUCTURE OF THE AXIS[1]. The **wood** contains no very broad medullary rays (their breadth not exceeding 4–6 cells), and has vessels with lumina of different sizes (maximum-diameter, ·033–·063 mm.). The vessels have simple perforations. The walls of the vessels are provided with bordered pits even where in contact with the parenchyma of the medullary rays. Spiral thickening or spiral striation of the vessel-wall has been observed in all the investigated species of the genera *Billardiera, Bursaria, Cheiranthera, Citriobatus, Marianthus, Pittosporum, Pronaya, Sollya*, and also in *Hymenosporum*. Wood-parenchyma does not take a prominent part in the formation of the wood. The pits of the wood-prosenchyma, which is sometimes provided with a few delicate division-walls, are simple, or at least possess only small indistinct borders. The **pith** consists of lignified cells. It not uncommonly becomes sclerotic in the outer part, which borders on the xylem (*Bursaria, Citriobatus*, &c., according to Grote).

Passing on to the structure of the **cortex**, it may first be pointed out with regard to the origin of the cork, that according to Van Tieghem, the phellogen appears in the outermost cell-layer of the primary cortex immediately below the epidermis of the branch in *Pittosporum, Ixiosporum*, and *Citriobatus*, in the third outermost cell-layer of the primary cortex in *Hymenosporum*, at the limit of primary and secondary cortex in *Sollya*. The cork-cells have wide lumina and stout walls. Phelloderm is also formed; if I understand Van Tieghem rightly, it is sometimes collenchymatous (*Pittosporum, Hymenosporum*); usually, however, it becomes sclerosed (*Pronaya, Ixiosporum, Citriobatus*, &c.). The primary cortex is generally collenchymatous, especially in its outer portions. The occurrence of secretory canals in the pericycle has already been discussed. On the outer side of the secretory canals one sometimes finds solitary bast-fibres (*Hymenosporum*) or arcs of bast-fibres (*Pronaya, Billardiera, Sollya, Cheiranthera*). The secondary cortex is completely destitute of sclerotic elements, but all the cells of the secondary bast have a tendency to become collenchymatous. The sieve-tubes have fairly small lumina and scalariform sieve-plates.

Literature: N. Müller, Pringsheim Jahrb., Bd. v, 1866–7, p. 387.—Van Tieghem, Canaux sécrét., Ann. sc. nat., sér. 5, t. xvi, 1872, pp. 163–8 and pl. xxi.—Vesque, Anat. de l'écorce, 1876, separate copy, p. 101.—De Bary, Vergl. Anat., 1877, especially p. 466.—Möller, Rindenanat., 1882, pp. 283, 284.—Vesque, Nouv. Arch. Mus. d'hist. nat., sér. 2, t. v, 1882–3, pp. 345–57 and pl. 21.—Van Tieghem, Struct. et affin. des P., Bull. Soc. bot. de France 1884, pp. 141–51 and Canaux sécrét. du péricycle dans la tige et la feuille des P., loc. cit., pp. 43, 44.—Solereder, Holzstruktur, 1885, p. 68.—Van Tieghem, Ann. sc. nat., sér. 7, t. i, 1885, pp. 30–7.—Leblois, Ann. sc. nat., sér. 7, t. vi, 1887, pp. 301–5.—Douliot, Ann. sc. nat., sér. 7, t. x, 1889, p. 359.—Lalanne, Feuilles persist., Act. Soc. Linn. Bordeaux, sér. 5, t. iv, 1890, p. 69 and pl. iv.—J. E. Weiss, Denkschr. Regensb. bot. Gesellsch. 1890, separate copy, p. 66.—Pax, in Natürl. Pflanzenfam., iii. Teil, Abt. 2 a, 1891, p. 107.—Becheraz, Sekretbild. schizog. Gänge, Diss., Bern, 1893, p. 33.

TREMANDREAE.

This small Order of plants, endemic in Australia, shows close agreement in the anatomical structure of its members.

The **leaves** are either flat or linear, and have a tendency to roll their margins inwards towards the lower side to a varied extent. The transverse section of the leaf thus frequently acquires a characteristic appearance, which may be made use of for distinguishing the species. The **mesophyll** is, as a rule, bifacial

[1] Chiefly according to Möller and Solereder, loc. cit.

in structure; the palisade-tissue one-layered. In *Tetratheca epiloboides*, Steetz, the entire mesophyll is composed of short-celled parenchyma (Chodat). The **epidermis** of the upper side of the leaf consists of large cells with straight or curved lateral walls and with a smooth or granulated cuticle. Gelatinization of the inner walls of the epidermal cells on the upper side of the leaf is a very widely distributed phenomenon (in *Tetratheca ciliata*, Lindl., *T. confertifolia*, Steetz, *T. ericifolia*, Sm., *T. nuda*, Lindl., *T. pilosa*, Labill., *T. thymifolia*, Sm.; *Platytheca Crucianella*, Steetz); it is not found in *Tremandra*, the leaves of which are more densely covered with hairs. **Stomata** are only present on the lower side of the leaf; in the fully developed leaf their guard-cells are surrounded by several irregularly arranged epidermal cells. Vesque states with regard to the development of the stomata, that the mother-cell of the guard-cells is probably formed by the first division. The vascular systems of the **veins** (generally those of the midribs also) are mostly embedded in the mesophyll; in *Tetratheca ciliata* the median vein is placed in connexion with the upper epidermis by means of a strand of collenchyma. Sclerenchyma is often absent in the principal vein, but it occurs on the upper side of the vascular bundles in the principal vein in *Tetratheca confertifolia*, *T. pilosa*, *T. thymifolia*, and weakly developed in *Tremandra stelligera*, R. Br.; in *Tetratheca ericifolia* it is replaced by collenchyma. The sclerenchyma attains the strongest differentiation in the fairly long leaves of *Platytheca Crucianella*, in which it not only forms considerable strands above and below the vascular bundles in the principal vein, but is also met with in the secondary veins. The **petiole** contains a single vascular bundle, with which two small lateral bundles are sometimes (*Tetratheca ericifolia*) associated.

Oxalate of lime is excreted in the form of ordinary solitary crystals, multiple-crystals of this form and also (primary cortex of *Tetratheca ciliata*) clustered crystals. Internal glands are absent.

The **hairy covering** consists of three forms of hairs: (*a*) simple unicellular hairs; (*b*) stellate hairs, and (*c*) glandular hairs. The simple, unicellular hairs are conical, pointed, thick-walled and with narrow lumina (*Tetratheca confertifolia*). The stellate hairs, the rays of which likewise have thick walls and narrow lumina, occur only in the genus *Tremandra* (*T. diffusa*, R. Br. and *T. stelligera*, R. Br.); they have a multiseriate stalk and a varied number of ray-cells, which are either spread out in one plane or radiate in different directions. The glandular hairs (glandular shaggy hairs = Drüsenzotten) likewise have a multiseriate stalk and a multicellular head; they occur especially in *Tetratheca* (*T. glandulosa*, Labill.), but also in *Platytheca* (*P. Crucianella*).

With regard to the structure of the **wood** the four species investigated (*Tremandra stelligera*, R. Br., *Platytheca galioides*, Steetz, *Tetratheca glandulosa*, Labill., and *T. ciliata*, Lindl.) agree in their narrow, 1–2-seriate medullary rays, the cells of which are elongated in the vertical direction, and in their small-lumened vessels (maximum diameter = ·02 to ·04 mm.), which chiefly exhibit large, simple pits on those walls which are in contact with the parenchyma of the medullary rays. In *Platytheca galioides* spiral thickening of the walls of the vessels occurs. The perforations of the vessels are simple, usually elliptical, rarely circular; specially elongated, elliptical, simple perforations are present in the neighbourhood of the primary wood, and in *Tremandra stelligera* irregular openings with two bars are also found here. In *Tetratheca* the wood-prosenchyma, which is sometimes finely spirally thickened, appears to bear exclusively bordered pits. In the two other genera, however, the wood-prosenchyma in part bears bordered pits (tracheides), in part simple pits.

As to the structure of the **cortex** in the single plant (*Tetratheca ciliata*), which was available to me at the time for investigation, a composite and continuous ring of sclerenchyma is resent at the outer limit

of the bast; in the almost leafless members of the Order (*Tetratheca nuda*, Lindl. and *T. juncea*, Sm.), palisade-parenchyma is developed in the primary cortex. The triangular branches of *Tetratheca juncea* further possess bundles of sclerenchymatous fibres at the three angles; a similar feature has also recently been observed by Chodat in *Tetratheca affinis*, Endl.

Literature: Vesque, Nouv. Arch. Mus. d'hist. nat., sér. 2, t. v, 1882–3, pp. 357–63 and pl. 22. —Solereder, Holzstr., 1885, p. 69.—Chodat and Balicka, Struct. des Tr., Bull. de l'Herbier Boissier, 1893, n. 7.—Chodat, in Natürl. Pflanzenfam., iii. Teil, Abt. 4, 1896, pp. 320, 321.

POLYGALEAE.

1. Review of the Anatomical Structure. The following features should be specially mentioned. The stomata are, as a rule, surrounded by several irregularly placed epidermal cells; more rarely approximations to the Rubiaceous or Cruciferous type are found. The midrib, and also the petiole, usually possess very simple structure, in that they contain only one vascular bundle. Oxalate of lime occurs in the form of ordinary solitary crystals and of clustered crystals. Internal secretory organs are wanting, apart from the 'lysigenous secretory cavities' and 'oil-cells,' which are stated by Chodat to occur in certain species of *Polygala* and which must be subjected to reinvestigation [1]; glandular hairs are likewise absent. The hairy covering is formed by simple unicellular hairs; an exception to this is afforded only by species of *Bredemeyera* and *Xanthophyllum*, which have simple uniseriate hairs. The wood contains narrow medullary rays, vessels with simply perforated end-walls, and wood-prosenchyma with typical bordered-pits.

The following features may be made use of for specific diagnosis: the varied structure of the mesophyll; the occurrence of sclerosed cells in the latter (layers of sclerosed spongy parenchyma in *Monnina speciosa*, Tr. et Pl., long sclerenchymatous cells in the palisade-tissue of *Moutabea guianensis*, Aubl.); the nature of the epidermis and its parts, such as formation of papillae (in species of *Muraltia*, *Polygala*, and *Securidaca*), the occurrence of hypoderm (in *Moutabea guianensis*), the arrangement of the stomata at right angles to the course of the veins (in *Krameria triandra*, Ruiz et Pav.); then the differentiation or the absence of sclerenchyma in the veins; the presence of broadened terminal tracheides (in species of *Badiera*, *Polygala*, and *Xanthophyllum*); the occurrence of peculiar granular or radiating masses resembling clustered crystals in species of *Polygala* which are composed of a substance not further known ('lysigenous oil-receptacles' of Chodat?).

In certain species of *Bredemeyera*, *Comesperma*, *Moutabea*, and *Securidaca*, thick portions of the stem exhibit concentric rings of growth (Fig. 23); the rings of secondary vascular bundles probably arise in the pericycle in every case.

2. Structure of the Leaf [2]. The **mesophyll** possesses a very varied structure, which in part is in agreement with the varied form and nature of the leaf. In *Mundtia brasiliensis*, St. Hil. and *Carpolobia alba*, Don the mesophyll consists of uniform tissue. The species with lanceolate or linear leaves, which are frequently rolled in towards the lower side at the margins,

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[1] I was not able to undertake this, as the material of the Munich Herbarium has been lent to Chodat for monographic work.

[2] Chiefly according to Vesque, Nouv. Archives du Mus. d'hist. nat., loc. cit. This work is based on an investigation of the genera, *Polygala*, *Badiera*, *Muraltia*, *Mundtia*, *Comesperma*, *Bredemeyera*, *Phlebotaenia*, *Securidaca*, *Carpolobia*, *Monnina*, *Xanthophyllum*, *Moutabea*, *Krameria*. Besides this, Chodat's investigation on the leaf-anatomy is also taken into consideration; however, it contains little that is new.

have either a bifacial (*Polygala pinifolia*, Lam., *Comesperma longifolia*, Steud., &c.) or a centric mesophyll (*Polygala polyphylla*, DC., *Muraltia obovata*, DC., *Comesperma rosea*, Steud., &c.). The mesophyll of the species with larger leaves is mostly bifacial, more rarely centric (*Krameria*). In the lanceolate leaves of *Muraltia ruscifolia*, Eckl. et Zeyh. an interesting case is met with, palisade-tissue being developed only on the lower side, while, below the upper epidermis, there are only cells which are poor in chlorophyll and have large cavities. In *Monnina polystachya*, Ruiz et Pav. and *M. revoluta*, H. B. K., the palisade-parenchyma has wavily-folded lateral walls; in *Monnina speciosa*, Tr. et Planch. one or two layers of the branched, spongy parenchyma lying immediately above the lower epidermis are sclerosed.

The **epidermal cells** mostly have straight lateral walls; more rarely the latter are undulated to a considerable degree, e.g. in *Comesperma volubilis*, Labill., *Bredemeyera brevifolia*, Klotzsch, *Monnina revoluta*, H. B. K., *Carpolobia alba*, Don, &c. The outer walls of the epidermal cells are usually flat, but sometimes arched outwards (*Polygala glauca*, E. Mey.); or those on the lower surface of the leaf bear knob-like papillae at the centre (*Securidaca rivinaefolia*, St. Hil., *S. oblongifolia*, Benth. et Hook., &c.), their walls being so strongly thickened in certain other species (*Polygala microphylla*, L. branch, *P. polyphylla*, DC., *P. pinifolia*, Lam.; *Muraltia Heysteria*, DC., *M. obovata*, DC.), that the papillae appear like strong cuticular projections. The outer wall of the epidermal cells is sometimes strongly thickened; this thickening now and then extends to the side-walls. The cuticle is smooth or granularly thickened (coarsely granular in *Polygala glauca*); striation of the cuticle is relatively rare (*Monnina loxensis*, Benth., *Muraltia brevicornu*, DC., *Badiera domingensis*, DC.). **Hypoderm** of two or more layers has been observed with certainty only on the upper side of the leaf of *Moutabea guianensis*, Aubl.; it may be added that this species possesses long, sclerosed, little-branched sclerenchymatous cells in the palisade-tissue.

The **stomata** occur either on both sides of the leaf or only on the lower side; in general this difference is only of specific value and is more or less in agreement with the centric or bifacial structure of the mesophyll. The developmental investigation of the stomatal apparatus in *Polygala virgata*, Thunb. has proved that the mother-cell of the guard-cells is cut off by the first division; but owing to later divisions in the neighbouring cells the stomatal apparatus of the Polygaleae varies in appearance. The guard-cells are, as a rule, surrounded in an irregular manner by several epidermal cells; in rather rare cases, however, only three neighbouring cells are present, or two, which are then placed parallel to the pore (the latter in *Securidaca bialata*, Benth., *S. volubilis*, L. and *Xanthophyllum vitellinum*, Bl.). In *Krameria triandra*, Ruiz et Pav., but not in *K. tomentosa*, St. Hil., the pore of the guard-cells is placed at right angles to the course of the vein, similarly to what occurs on the branches of certain Tamariscineae.

The following facts should be mentioned with regard to the structure of the **veins**. The species with small leaves, as a rule, have no sclerenchyma in the veins; *Muraltia Heisteria*, DC. and *M. heterophylla*, E. Mey. afford an exception to this, the vascular bundles of the midribs being accompanied by considerable bundles of bast-fibres. In the large-leaved species sclerenchyma is also found accompanying the smaller veins, either only in connexion with the phloem (species of *Securidaca*, *Monnina polystachya* and *M. speciosa*), or on both sides (species of *Bredemeyera*), or forming a ring (in *Xanthophyllum vitellinum*, Bl. and *X. flavescens*, Roxb.). In *Phlebotaenia cuneata*, Griseb. vertically transcurrent veins are present, for in this case sclerosed tissue adjoins the bundles of sclerenchyma belonging to both sides, and extends as far as the epidermis. Enlarged terminal tracheides have been observed in *Polygala*

ephedroides, Burch., *Badiera domingensis*, DC., *Xanthophyllum flavescens*, Roxb. and *X. vitellinum*, Bl. The midrib mostly contains a single round, band-shaped, or horse-shoe-like vascular bundle. Two bundles are present in *Moutabea* only; of these the upper one has reversed orientation.

Similarly, according to Chodat and Komaroff, the **petiole**, even in large-leaved species, is as a rule traversed by a single vascular bundle only, which in *Polygala* has nearly always a crescent-shaped transverse section. In species of *Securidaca*, in *Bredemeyera* and in *Polygala venenosa*, a transverse section of the fibro-vascular system shows a ring which is only slightly open above, in *Moutabea*, *Carpolobia*, *Afzeliana* and some species of *Xanthophyllum* there is a closed ring. The vascular system becomes still more complicated in *Xanthophyllum vitellinum*, &c.; on this subject further details are to be found in another place.

Oxalate of lime is deposited in the leaf and axis mostly in the form of ordinary solitary or clustered crystals. In the bast of Radix Ratanhiae (*Krameria triandra*, Ruiz et Pav.) crystal-sacs occur with several prismatic solitary crystals in the same cell. According to the investigations hitherto undertaken, oxalate of lime appears to be wanting in some genera (*Xanthophyllum*, *Bredemeyera*). In this connexion reference should be made to the granular or radiating masses resembling clustered crystals and composed of a substance, on the nature (resinous?) of which nothing further is known; Vesque has met with these masses in the mesophyll of certain species of *Polygala* (*P. adenophylla*, St. Hil., *P. 'cordata,' P. myrtifolia, P. pinifolia*, Lam., *P. rosmarinifolia*, Eckl. et Zeyh., *P. speciosa*); they are insoluble in hydrochloric acid, soluble in potash-solution and in alcohol. We may mention as probably identical with these masses the excretions, which Chodat has described as[1] lysigenous oil-receptacles in many South American species of *Polygala* (e.g. *P. glandulosa* or *P. macradenia*).

The **hairy covering** consists almost exclusively of unicellular hairs. Only in *Bredemeyera* and *Xanthophyllum* are the hairs uniseriate, owing to subsequent septation. Glandular hairs are absent.

The form of the unicellular hairs differs somewhat in the different species as also does the nature of their walls. Thus the hairs are either long and pointed, in this case sometimes (*Polygala coriacea*, St. Hil., *Comesperma volubilis*, Labill., *C. ramosissima*, Steud., *Monnina*) narrowed at the base; or they are short and conical and are then occasionally curved into a hooked form (*Comesperma longifolia*, Steud., *Badiera domingensis*, DC.). The wall of the hair is, for the most part, little thickened, sometimes even very thin (*Polygala coriacea*). But in certain species of *Mundtia*, *Muraltia*, and *Krameria*, the wall of the hair is thick and the cell-lumen almost obliterated. Lastly, *Monnina* has, in addition, fairly short unicellular hairs considerably thickened at the tip. The wall of the hair is very frequently provided with knob-like thickenings on its outer side; but not always, e.g. not in most of the species of *Polygala*, in *Muraltia ruscifolia*, Eckl. et Zeyh., in *Monnina*, *Krameria*, &c.

3. STRUCTURE OF THE AXIS. Regarding the structure of the **wood** the following facts should be specially mentioned as shown by my own investigation of species of *Muraltia*, *Polygala*, and *Securidaca*, as well as by that of Chodat. The xylem always forms a closed ring, even in the herbaceous species investigated by Chodat. The medullary rays are narrow, and their cells are elongated in the vertical direction. The vessels, which are not numerous, vary in the size of their lumina (maximum diameter in *Muraltia ononidifolia*, Eckl. et Zeyh. ·018 mm., in *Securidaca Tavoyana*, Wall. ·08 mm.). The perforations are simple;

[1] Secretory organs of other types are wanting in the leaves of the Polygaleae, although Spach attributes a milky sap to some of them; as to the oil-cells stated by Chodat to occur in the wood of *Polygala Senega*, see under the structure of the wood.

the walls of the vessels are provided with bordered pits even where they are in contact with the parenchyma of the medullary rays. Spiral thickening of the vessel-wall has been observed in *Polygala Eckloniana*, Presl and *Muraltia ononidifolia*. In all members of the Order the wood-prosenchyma, which forms the groundwork of the xylem, has bordered pits, even in *Krameria triandra*; this favours the view that *Krameria* belongs to the Polygaleae and not to the Caesalpinieae (cf. under that Family). According to Chodat, wood-fibres with simple pits are sometimes intermingled, in relatively small quantity, with the main mass of wood-prosenchyma, which has bordered pits. I leave the interpretation of the oil-cells, described by Chodat in the wood of *Polygala Senega*, an open question.

The **pith** consists of lignified or unlignified cells. In the second case the shoot frequently becomes fistular. Stone-cells have been observed in the pith of *Polygala macroptera*, DC. and species of *Securidaca*.

With regard to the structure of the **cortex**, the following is to be gathered from Chodat's statements. The epidermis shows manifold differences with respect to the nature of its walls. It is strongly thickened in xerophilous species, but is thin-walled in those provided with leaves adpressed to the stem.

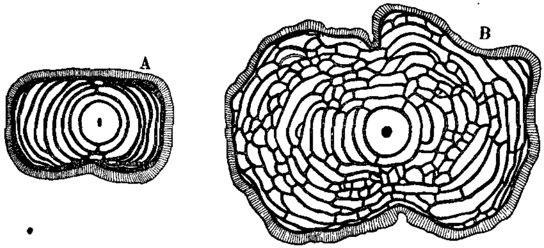

FIG. 23. Anomalous pieces of stem of: A, *Securidaca Sellowiana*, Klotzsch; B, *Securidaca lanceolata*, St. Hil. Both figures natural size; xylem-portions white, bast-portions and cortical portions shaded.—After H. Schenck.

Horizontal division-walls have been observed in the epidermal cells of species of *Securidaca*; papillose differentiation of the epidermis in *Polygala polygama* and *P. Laureola*. In *Moutabea guianensis* cork, made up of stone-cells, is found immediately below the epidermis. The primary cortex is frequently collenchymatous. It contains stone-cells in *Polygala ligustroides*, groups of fibres in the herbaceous shoots of *Securidaca* and *Comesperma*. Identical groups of fibrous cells occur also in the ribs which are present on the stem in some species, e.g. *Polygala irregularis* and *Comesperma volubilis*, while the wings of the stem of *Polygala triquetra* are only filled with cortical parenchyma. Hard bast is present in the pericycle, and either (*Polygala setacea*) forms small isolated bundles only, or a narrow ring (*Polygala adenophylla*, *P. ambigua*, *P. leptostachys*) or a very broad ring (*Securidaca*). The individual bast-fibres are either thick-walled and have narrow lumina, being in that case stratified (*Polygala macroptera*), or have fairly wide lumina (*Polygala supina*). Secondary hard bast has been observed in some cases.

Anomalous structure of the axis is present in some members of the Order in the form of successive rings of growth. This was first described by the older authors in *Securidaca volubilis* and *Comesperma*. To the species presenting this anomaly we must add: according to H. Schenck, *Brede-*

meyera, *Schenckiana*, Chodat, *Securidaca lanceolata*, St. Hil. and *S. Sellowiana*, Klotzsch, and according to Chodat, *Moutabea guianensis*. *Catocoma lucida*, Benth. (=*Bredemeyera lucida*) differs from *Bredemeyera Schenckiana* in having normal structure, according to Crüger. The anomaly in question only appears fairly late, and is therefore not usually to be met with in the branches of herbarium-material. The formation of the secondary bundles, according to H. Schenck, takes place in the parenchymatous pericycle on the inner side of the bundles of primary hard bast; with this De Bary's statement (origin of the secondary bundles in the outermost part of the bast) may in some measure be brought into agreement. As to the general appearance of the transverse section of the axis it may be added that the rings of wood in *Securidaca* are more or less frequently traversed by radial bridges of the same thin-walled parenchyma of which the intermediate tissue between the successive rings of bundles consists (they occur, though not very abundantly, in *Securidaca Sellowiana*, Fig. 23, *A*, but are specially abundant and irregular in *S. lanceolata*, Fig. 23, *B*). This also holds good for *S. volubilis*, according to Crüger's figure, while in *Bredemeyera Schenckiana* the rings of wood are broad and, as far as is known, continuous.

4. Structure of the Root. With regard to this it need only be mentioned that the successive rings of bundles, according to Crüger, also occur in the root of *Securidaca volubilis*, and that the irregular shape of the mass of wood in Radix Senegae (which, as is well known, is fissured at many points, and is excavated especially in the region opposite the so-called keel) is caused, according to Linde, by the intrusion of broad and, for the most part, thin-walled medullary rays.

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VOCHYSIACEAE (incl. Trigoniaceae).

1. Review of the Anatomical Features. The following characters are common to the Vochysiaceae, with the exception of the Trigoniaceae (i.e. of the genera *Trigonia*, *Trigoniastrum*[1] and *Lightia*): (*a*) the occurrence of intraxylary soft bast, which is differentiated in the form of a ring of phloem in the medullary sheath or in the form of medullary phloem-islands; and (*b*) the simple pitting of the wood-prosenchyma. The Trigoniaceae, on the other hand, possess simple collateral vascular bundles and wood-prosenchyma with bordered pits. Simple perforations of the vessels are present in all the Vochysiaceae (including the Trigoniaceae), and the wood-parenchyma is always more abundantly developed than is commonly the case. The genus *Erisma* is distinguished from the others by the possession of interxylary phloem. The cork takes its origin either in a superficial cell-layer of the cortex (*Salvertia*, *Vochysia*, Trigoniaceae), or in the pericycle (*Erisma*, *Qualea*). The stomata are either surrounded by several ordinary epidermal cells (*Vochysia*, *Erisma*, *Salvertia*), or

[1] The genus *Trigoniastrum*, which is included by Bentham and Hooker in the Polygaleae, has been removed by Chodat (Bulletin de l'Herbier Boissier, t. iii, 1895, p. 136 et seq.) to the Trigoniaceae and is therefore dealt with here.

are accompanied by subsidiary cells, which lie parallel with the pore (*Callisthene, Qualea*, and especially *Trigonia*). Oxalate of lime is deposited in the form of solitary (*Qualea, Erisma*), or clustered crystals (*Callisthene, Vochysia, Salvertia, Trigonia*), or clustered and solitary crystals (Trigoniaceae). In this Order the occurrence of mucilage or gum is a very widely distributed phenomenon. Epidermal cells of the leaf with mucilaginous inner membranes have been observed in species of *Callisthene, Qualea, Salvertia, Trigonia*, and *Trigoniastrum*, mucilaginous hypoderm-cells in *Lightia licanioides*, Spruce, mucilaginous cells in the tissue of cortex and pith in *Qualea*, lysigenous gum-canals in the pith of the branch, petiole and leaf-veins in the genera *Salvertia, Vochysia*, and *Erisma*. The hairy covering consists only of clothing hairs. Glandular hairs are absent, apart from the large nectaries occurring above the stipules in species of *Qualea*. The clothing hairs are unicellular throughout. In *Erisma* several of these are united into tufted hairs. Special forms of simple unicellular hairs are the one-armed trichomes of *Salvertia convallariaeodora*, St. Hil., and the two-armed hairs of certain, but not all, species of *Vochysia*. Among specially noteworthy anatomical characters, which, however, only occur in certain species and are characteristic of these only, the following should be mentioned: the small-celled epidermis of the leaf of *Erisma violaceum*, Mart. and *Lightia licanioides*, Spruce; the typically two-layered epidermis on the upper side of the leaf of certain species of *Qualea* and *Vochysia*; the occurrence of a large-celled, one-layered hypoderm on the upper side of the leaf of *Lightia licanioides*; the papillose epidermis on the lower side of the leaf of *Qualea glauca*, Warm.; the occurrence or absence of sclerenchyma accompanying the vascular bundles of the veins; the much-elongated, spirally-thickened storage-tracheides in the mesophyll of *Vochysia rufa*, Mart.; the branched sclerenchymatous cells in the leaf-tissue of *Lightia licanioides*; the diverse differentiation of the intraxylary phloem; the occurrence of sclerenchyma in the pith; the septation of the wood-prosenchyma by means of thin division-walls; the inversely orientated medullary bundles in an undetermined species of *Trigonia*, &c. How far the bifacial leaf-structure, the straight lateral walls of the epidermal cells of the leaf, the restriction of the stomata to the lower leaf-surface, and the vertical transcurrence of the smaller veins (features almost all[1] of which have so far been met with in all the species investigated), are of importance for the diagnosis of the Order, can only be determined by investigation of more numerous species.

2. Structure of the Leaf. This has been investigated by Wille in *Vochysia oppugnata*, Warm., *V. laurifolia*, Warm., *Qualea Glaziovii*, Warm., and *Q. Gestasiana*, St. Hil.; by me in *Callisthene fasciculata*, Mart., *Qualea glauca*, Warm., *Erisma violaceum*, Mart., *Vochysia rufa*, Mart., *Salvertia convallariaeodora*, St. Hil., *Trigonia laevis*, Aubl., and *T. Volkensiana*, K. Schum.; lastly by Barth in numerous species of *Trigonia, Lightia licanioides*, Spruce, and *Trigoniastrum hypoleucum*, Miq.

The structure of the leaf in the species named is bifacial; in *Qualea glauca* alone the spongy parenchyma is partly differentiated like palisade. In the species examined by me the **epidermal cells** on both sides of the leaf have a polygonal outline in surface view. In *Erisma violaceum* the epidermal cells of the upper side of the leaf are characterized by a surprisingly small contour and are, in part, divided by rather thin secondary vertical walls; those of *Lightia licanioides* (according to Barth) are also small. In *Vochysia rufa* the epidermis of the upper side of the leaf becomes two-layered owing to horizontal division-walls, the cells of the upper and lower layers corresponding throughout.

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[1] *Trigonia* and apparently also the rest of the Trigoniaceae have no 'vertically transcurrent smaller veins.'

The same is the case, according to Wille's figures, in *Qualea Glaziovii* and *Q. Gestasiana*, and locally, according to Barth, in *Lightia licanioides* and *Trigoniastrum hypoleucum*. *Lightia licanioides* possesses a one-layered, large-celled hypoderm beneath the locally doubled epidermis. The occurrence of epidermal or hypodermal cells with mucilaginous inner membranes is widely distributed. I have met with mucilaginous epidermal cells in *Callisthene fasciculata*, *Qualea glauca*, *Salvertia convallariaeodora*, *Trigonia laevis* and *T. Volkensiana*, in specially large numbers in the two last-named species and present on both sides of the leaf; to judge by Wille's figure, they are also found in *Qualea Gestasiana*, and, according to Barth, in most of the species of *Trigonia* investigated by him and in *Trigoniastrum*. In *Lightia licanioides* the cells of the hypoderm are mucilaginous. The **stomata** are restricted to the lower epidermis of the leaf in all investigated species. According to Wille, the mother-cell of the guard-cells in *Vochysia oppugnata* originates on the appearance of the first division-wall. Hence in *Vochysia* the pair of guard-cells is surrounded by several ordinary epidermal cells. This applies also to the species of *Vochysia*, *Erisma*, and *Salvertia* investigated by me. The stomatal apparatus of *Callisthene*, *Qualea*, and *Trigonia*, on the other hand, judged by the mature structure, is to be referred to the Rubiaceous type; the subsidiary cells parallel to the pore are especially distinct in the species of *Trigonia*. It should also be stated that the cells of the lower epidermis of the leaf of *Qualea glauca* are papillosely differentiated. The vascular bundles of the larger and smaller **veins** in *Qualea glauca*, *Erisma violaceum*, *Vochysia rufa*, *Salvertia convallariaeodora* and *Trigonia laevis* are provided with a sclerenchymatous investment of variable strength, but this is absent in *Callisthene fasciculata* and *Trigonia Volkensiana*. A point of more importance than either this feature or the appearance of the midrib and petiole in transverse section (as to which, Wille's statements regarding the species investigated by him may be referred to) is the fact that the smaller veins are vertically transcurrent in all the species investigated by me (excluding the two species of *Trigonia*), for tissue which is usually thin-walled and colourless, more rarely sclerotic, adjoins the vascular bundles of these veins and extends as far as the epidermis on both sides. Here we must also note the occurrence of spirally thickened storage-tracheides in the leaf of *Vochysia rufa* and of branched sclerenchymatous fibres in the leaf of *Trigoniastrum hypoleucum*. The storage-tracheides of *Vochysia rufa*, which are in connexion with the tracheae of the terminations of the veins, are of tubular shape, and often traverse almost the entire thickness of the leaf in a perpendicular direction, their upper ends extending close to the upper epidermis.

Oxalate of lime is deposited in the leaves in the form of solitary and clustered crystals. In the species of *Qualea* and *Erisma* cited, only ordinary solitary crystals have been observed, in the species of *Callisthene*, *Vochysia* and *Salvertia*, only clustered crystals, but in the Trigoniaceae both solitary and clustered crystals occur.

The **hairy covering** consists as a rule of simple unicellular hairs (*Callisthene*, *Qualea*, *Vochysia*, *Salvertia*, Trigoniaceae). These unicellular hairs exhibit differences in the first place as regards their length and the thickness of their walls, and their straight or undulated course. The simple unicellular hairs of *Qualea glauca* and *Vochysia rufa* are noteworthy, as having a suddenly narrowed and contracted base, which is wedged in between the epidermal cells; those of *Salvertia convallariaeodora* must be referred to the one-armed hairs. A transition is afforded through the one-armed hairs to the unicellular two-armed hairs of certain but not of all (see above) species of *Vochysia*. Wille states that the latter occur in *V. laurifolia* and *V. oppugnata*; I have met with them also in *V. vismiaefolia*, Spruce. A further special form of hair occurs in the genus *Erisma*, namely, **tufted** hairs; these are composed of a

variable number of ray-cells. Real glandular hairs are absent. On the other hand, large extrafloral nectaries, which appear to excrete a gummy secretion and are placed singly above the stipules, have been observed by Wille in *Qualea laurifolia* and *Q. oppugnata*; their structure requires further investigation.

3. STRUCTURE OF THE AXIS. **Intraxylary soft bast** is characteristic of the true Vochysiaceae; it has been demonstrated by Wille and by me in twenty-nine species of the genera *Salvertia, Vochysia, Erisma, Qualea,* and *Callisthene*. This inner soft bast, to the more detailed description of which I shall return immediately, is wanting, on the other hand, in the Trigoniaceae, which, according to Warming's view, must be separated from the Vochysiaceae, and in correspondence with this have recently been raised by Petersen to the rank of an independent Order. Almost all the species of *Trigonia* as well as *Trigoniastrum* and *Lightia* have quite normal stem-structure (branch); only one species of *Trigonia*, mentioned by Petersen but not determined, forms an exception to this, inasmuch as an interrupted ring of vascular bundles is met with in the pith of this plant, and shows inverse orientation, i.e. with xylem outwards and phloem inwards. The inner soft bast is developed in different ways in the genera quoted above. It is present either in the form of islands scattered in the pith or as a ring in the medullary sheath, or lastly, it occurs in both forms. All the species of *Vochysia* and *Salvertia* hitherto investigated have only islands of soft bast in the pith. In a certain number of the species of *Qualea*, e.g. *Q. Glaziovii*, Warm., there is a ring of soft bast at the margin of the pith; in other species of the same genus, e.g. *Q. Gestasiana*, St. Hil., islands of soft bast occur in the pith in addition to the ring. In *Callisthene* only the ring of soft bast is present. Lastly, in *Erisma*, either medullary islands as well as a ring of soft bast (*E. calcaratum*, Warm.) have been observed, or the former alone (*E. violaceum*, Mart., *E. micranthum*, Spruce). All the preceding detailed statements can be shortly summarized by saying that, according to investigations hitherto carried out, groups of soft bast in the pith are not lacking in any species of *Vochysia, Salvertia* or *Erisma*, nor the ring of soft bast in the medullary sheath in any species of *Callisthene* or *Qualea*.

With regard to the **pith**, mention should also be made of the presence of groups of sclerenchyma, which are described by Wille for species of *Salvertia, Vochysia, Erisma,* and *Qualea*. They sometimes show a relation to the groups of soft bast.

Regarding the structure of the **wood** the following statements are based on what is found in the species of the genera *Vochysia, Qualea, Erisma,* and *Trigonia* investigated by me, as well as on Barth's statements regarding the Trigoniaceae. The medullary rays are 3–5-seriate, and their cells are elongated in part in the vertical, in part in the radial direction. The vessels are isolated, or in radial series; their lumina are round and have a maximum diameter of ·051–·09 mm. The perforations of the vessels are simple and circular or elliptical. On the wall of the vessel, where it is in contact with the parenchyma of the medullary rays, bordered pits occur, or, besides the latter, transitions to simple pits (*Erisma*). The bordered pits of the vessel-wall sometimes (*Callisthene, Erisma, Vochysia*) possess the sieve-plate-structure discovered by Bengt Jönsson (Heiden). The wood-prosenchyma bears bordered pits in the Trigoniaceae, elsewhere simple pits; in the latter case it is sometimes (*Qualea dichotoma*, Warm.) septate. Wood-parenchyma is developed fairly abundantly in all the members of the Order; chambered crystal-parenchyma with solitary crystals has been observed in *Qualea dichotoma* and *Erisma violaceum*, Mart.

The four species of *Erisma* investigated (*E. calcaratum*, Warm., *E. micranthum*, Spruce, *E. uncinatum*, Warm. and *E. violaceum*, Mart.) are characterized by a special anomalous structure of the wood—interxylary phloem. The islands

of soft bast in the wood, according to Wille and Chodat, are given off by the cambium on its inner side [1].

The researches of Wille and Barth give some information as to the structure of the **cortex**. The formation of cork takes place subepidermally in the Trigoniaceae, near the epidermis in *Salvertia* and *Vochysia*, on the inner side of the sclerenchymatous pericycle in *Erisma* and *Qualea*. Sclerenchyma is present in abundance in the cortex. In the pericycle it sometimes forms an almost closed ring (*Qualea Glaziovii*, Warm.), or a composite and continuous sclerenchymatous ring (Trigoniaceae). Sclerenchyma is frequently also developed in the secondary bast (Trigoniaceae, *Qualea*, *Vochysia*).

Secretory organs, apart from tannin cells, which are widely distributed in the pith and cortex, are represented by lysigenous mucilage-canals and mucilage-cells, found in the axis. The mucilage-canals are, as a rule, present only in the pith. They run for a distance of 1 or 2 internodes in the stem, and then pass without anastomoses into the petiole, from which they can sometimes be traced into the larger veins of the leaf. In the petiole and in the veins the mucilage-canals are situated on the inner or upper side, as the case may be, of the xylem, and only exceptionally (in the petiole of *Vochysia oppugnata*) occur in the bast also. Mucilage-canals have been observed in the species of *Salvertia*, *Vochysia*, and *Erisma* enumerated below [2]; whether they have specific or generic value, requires to be more fully tested. The mucilage-cells (cells with mucilaginous membrane or groups of such cells) are present in many species of *Qualea*, e.g. *Q. Gestasiana*, St. Hil., in the primary cortex and in the pith of the axis as well as in the parenchyma of the petiole; the mucilage-canals mentioned above are absent in *Qualea*. The gum-canals of the wood, stated by Wille to occur in *Q. Lundii*, Warm., appear to be of a pathological natnre. Lastly, it remains to be mentioned, that mucilage-containing, secretory spaces arise by the disintegration of groups of cells in the stipules of *Vochysia oppugnata*.

Literature: Wille, Om stamm. og blad. bygn. hos Vochysiac., Oversigt Videnskab. Selsk. Kjøbenhavn 1882, pp. 180–205, Tab. vii–xi, with French *résumé*, pp. 13–20.—Solereder, Holzstr., 1885, pp. 70–3.—Scott and Brebner, Anat. and hist. of *Strychnos*, Annals of Bot. 1889, pp. 295–7.—Chodat, Atti del Congr. internaz. Genova 1892, p. 144 et seq.—Heiden, Anat. Charakt. d. Combretaceen, Diss., Erlangen 1893, p. 16 note.—H. Schenck, Anat. d. Lianen, 1893, p. 130.—Petersen, in Natürl. Pflanzenfam., iii. Teil, Abt. 4, 1896, pp. 309, 310 and 313.—Barth, Anat. comp. de la tige et de la feuille des Trigoniacées etc., Bull. de l'Herbier Boissier, t. iv, 1896, pp. 483–96.

FRANKENIACEAE.

This small Order, composed solely of strand- and desert-plants and comprising the three genera *Frankenia*, *Beatsonia*, and *Niederleinia*, is especially characterized anatomically by the possession of extremely peculiar epidermal glands (Fig. 24), which frequently secrete certain salts, and which agree in their structure with the glands of the Tamariscineae and Plumbagineae. The hairy covering is composed of simple unicellular trichômes, which are sometimes grouped together in tufts. Oxalate of lime occurs in the form of clustered crystals. In the woody species the wood consists of vessels with simple perforations and of wood-prosenchyma with simple pits, while distinct

[1] Interxylary phloem also occurs in the root of *Erisma* and there forms small groups of cells, enclosed in islands of the unlignified parenchyma; the details of its origin have yet to be determined.

[2] *Salvertia convallariaeodora*, St. Hil.; *Vochysia bifalcata*, Warm., *V. cinnamomea*, Pohl, *V. divergens*, Pohl, *V. elliptica*, Mart., *V. emarginata*, Vahl, *V. laurifolia*, Warm., *V. oppugnata*, Warm., *V. quadrangulata*, Warm., *V. rufa*, Mart., *V. thyrsoidea*, Pohl, *V. Tucanorum*, Mart., *V. vismiaefolia*, Spruce; *Erisma micranthum*, Spruce.

medullary-ray-parenchyma is wanting. The cork arises subepidermally in the case investigated (*Frankenia laevis* according to Douliot).

In amplification of this short diagnosis, the following facts may be added. The leaves which are usually revolute at the margin (rolled leaves) show a very varied appearance in transverse section, which, if always taken at the same point (the middle of the leaf), can be made use of as a specific character. In most members of the Order, even in *Niederleinia juniperoides*, Hieron., the **mesophyll** is bifacial in structure; the palisade-cells are found on the upper side, usually taking up half the thickness of the leaf, and are secondarily divided by transverse walls. Subcentric structure of the parenchyma of the leaf occurs in *Beatsonia portulacifolia*, Roxb. and in some few species of *Frankenia*, which likewise have flat leaves, e.g. *F. grandifolia*, Cham. et Schlecht., *F. hirsuta*, L., *F. Nicolitiana*, Gay, and *F. persica*, Jaub. et Spach. The rolled leaves of *F. thymifolia*, Desf., *F. Reuteri*, Boiss., and *F. triandra*, Remy, show a special distribution of the palisade-tissue. In these three species the palisade-parenchyma is found in all parts of the leaf which are turned towards the light. In *F. thymifolia* and *F. Reuteri* the geometrically lower side of the leaf exhibits a groove to the right and left respectively of the projecting midrib; palisade-tissue is present on the geometrically upper side and on the leaf-margins which are curved downwards, as well as in the downwardly projecting midrib; in *F. triandra*, in which the leaves are grooved on the lower side and have their geometrically upper side adpressed to the branch, the palisade-tissue is wanting on that side, and is developed only on the geometrically lower side, where it is present even at the bottom of the grooves. In the species with rolled leaves the **stomata** are mostly found only in the grooves of the lower side; sometimes, however, they also occur on the upper side of the leaf, e.g. in *F. triandra*. Their guard-cells are surrounded by several irregularly placed epidermal cells. The **veins** are embedded in the tissue of the leaf. The principal veins vary in degree of development, a point which Vesque makes use of for specific diagnosis in *Frankenia*. Sclerenchyma may accompany the vascular bundles of the leaf, or may be absent. According to Niedenzu the varied differentiation or the absence of the mechanical system in the veins affords a good character for distinguishing species, which are difficult to separate by means of their floral morphology. According to Vesque and Niedenzu the following plants have no hard bast or only a few sclerenchyma-fibres accompanying their vascular bundles: *Frankenia bracteata*, Turcz., *F. corymbosa*, Desf., *F. ericifolia*, Chr. Sm., *F. glomerata*, Turcz., *F. hispida*, DC., *F. laevis*, L., and *F. pulverulenta*, L.; while *F. capitata*, Webb et Berth., *F. Palmeri*, Wats., *F. revoluta*, Forsk., and *F. thymifolia*, Desf., as well as *Niederleinia*, have a more or less extensive development of hard bast. According to Niedenzu sclerenchyma-fibres also occur free in the mesophyll in *F. revoluta*; in *F. triandra* they form 'marginal bast' at the edge of the leaf.

Oxalate of lime, which, as has already been noted above, only occurs in the form of clustered crystals, is found in special abundance in the mesophyll of *F. intermedia*, DC., *F. fruticulosa*, DC., &c.; in other species it appears to be absent.

The **hairy covering** consists of unicellular, simple, sometimes tufted hairs; as further epidermoid structures, the peculiar glands may be mentioned. The simple hairs are sometimes thick-walled and in that case are pointed at the end and have a smooth, finely striate or punctate surface; or they may be thin-walled and are then blunt at the end. Sometimes both forms occur on the same leaf, the thick-walled hairs on the upper side, the thin-walled hairs in the grooves of the leaf. The length of the simple hairs also varies; sometimes they are short and in that case often project like papillae, each springing from the middle of the outer wall of an epidermal cell; sometimes, however, they

are of considerable length. The peculiar glands of the Frankeniaceae (Fig. 24, *A–C*) have been investigated especially by Vuillemin and Volkens in the genus *Frankenia*. But they are found also in the two other genera, *Beatsonia* and *Niederleinia*. These glands, like those of the Tamariscineae and Plumbagineae, do not project in the form of hairs but lie approximately in the plane of the epidermis, as in *Frankenia*, or at the bottom of a fairly deep pit in the leaf, as in *Niederleinia*. According to my investigations on *Frankenia thymifolia*, Desf., *F. pulverulenta*, L. and *Beatsonia portulacifolia*, Roxb. (which are not quite in agreement with the statements of Vuillemin and Volkens), these glands consist of a group of six (not four) cells, which have apparently been derived by division from a single epidermal cell. In the formation of the gland, an epidermal cell first divides by a vertical wall into two daughter-cells; each of the latter then further divides into two cells by an oblique wall directed towards the basal line of the common division-wall. Each of the two upper cells divides again by a similarly directed oblique wall, so that a glandular apparatus consisting of four secretory gland-cells and a pair of subsidiary cells arises (see Fig. 24, *B–C*). In surface-view (Fig. 24, *A*) one sees only the two

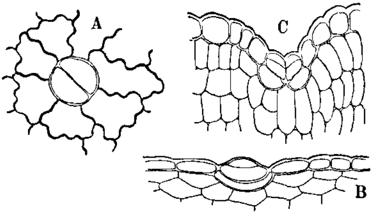

FIG. 24. Gland of *Frankenia pulverulenta*, L.: A, in surface-view; B, in a section cut parallel to the common vertical wall of the two gland-cells; C, in a section cut perpendicularly to this vertical wall.—Original.

uppermost gland-cells, which together resemble a pair of guard-cells, from which, however, they can be distinguished without difficulty. Sometimes paired glands are found in considerable numbers, e.g. in *E. floribunda*, Pom. It has already been indicated above, that the glands in question secrete a mixture of certain salts, which in part at least are hygroscopic, and which cover the vegetative parts of the plant, and that by means of this covering and the subsequent absorption of water, they are of great significance for the existence of plants of dry habitats, like the Frankeniaceae.

It should be added to what has been stated above regarding the structure of the wood (*Frankenia strigosa*, Presl, *Beatsonia portulacifolia*, Roxb.), that the vessels are round and have small lumina (maximum diameter = ·018–·03 mm.).

Literature: Hieronymus, *Niederleinia juniperoides* etc. (Spanish), in Lorentz and Niederlein, Enum. plant. Argent., 1881.—Vesque, Hist. syst. de la feuille des Caryophyllacées, Ann. sc. nat., sér. 6, t. xv, 1883, pp. 119–29, pl. vii.—Solereder, Holzstruktur, 1885, p. 73.—Volkens, Fl. ägypt. Wüste, Sitz.-Ber. Berliner Akad. 1886, and Aegypt.-arab. Wüste, 1887, pp. 108, 109 and Taf. v.—Vuillemin, Glandes épidermiques, Ann. sc. nat., sér. 7, t. v, 1887, pp. 168–73 and pl. iv.—Marloth, Salzabscheid. Drüsen etc., Ber. deutsch. bot. Gesellsch. 1887, p. 323, and Volkens, Erwid., loc. cit., 1887, p. 434.—Douliot, Ann. sc. nat., sér. 7, t. x, 1889, p. 344.—Goebel, Pflanzenbiol. Schild. ii, 1891, p. 13 and Tab. xii.—Niedenzu, in Natürl. Pflanzenfam., iii. Teil, Abt. 6, 1895, pp. 284, 285.—Warming, Halofyt Stud., K. Danske Vid. Selsk. Skr. 1897, p. 188.

CARYOPHYLLEAE.

1. Review of the Anatomical Features. The Order is characterized by certain very noteworthy anatomical features. In the first place we must mention the nature of the stomatal apparatus, the pair of guard-cells being surrounded by two subsidiary cells placed transversely to the pore (Fig. 25, *C*). Oxalate of lime is mostly excreted in the form of clustered crystals. Ordinary large solitary crystals have not been observed; but, on the other hand, finely divided crystal-sand is found in *Acanthophyllum*. The hairy covering consists of simple, uniseriate hairs and of similarly constituted glandular hairs with a unicellular glandular head (Fig. 25, *A–B*). Sclerenchyma is almost always wanting in the veins of the leaf; in the cortex, on the other hand, a sclerenchymatous strengthening ring is present in the majority of the genera. The development of cork is mostly internal, rarely superficial. The xylem of the woody genera contains wood-prosenchyma with simple pits; distinct medullary rays are wanting. The wood-vessels have simple perforations. Even in the woody species unlignified tissue frequently takes part in the formation of the xylem-mass. Lastly, the following features are also worthy of note: the fission of the xylem-mass in certain species of *Acanthophyllum*, this being connected with the development of inversely orientated, medullary vascular bundles; the extrafascicular origin of secondary bundles in the root (in part also in the stem) of species of *Spergularia* and *Polycarpaea*; and the peculiar concentric stratification of the xylem-mass in the species of *Acanthophyllum* having normal structure, by means of narrow rings of unlignified parenchyma, which includes spiral tracheae with narrow lumina.

2. Structure of the Leaf[1]. In very many cases the structure of the leaf is centric (*Silene inflata, Dianthus Caryophyllus, Arenaria longifolia*, &c.), but is sometimes bifacial (*Alsine pinifolia*). In leaves with centric structure the middle of the mesophyll is frequently occupied by aqueous cells, which surround the fibro-vascular system, and are also met with in the primary cortex of the branch (*Polycarpaea fragilis*, Del.). The **epidermal cells** have straight or undulated lateral walls. In long leaves the epidermal cells are sometimes very much elongated, and in that case not always in the direction of the midrib (as in *Sagina Villarsii, Drypis spinosa*, L., &c.), but sometimes (*Silene fruticosa*, L.) in the transverse direction. Papillose differentiation of the epidermis has been observed locally in *Gypsophila Rokejeka*, Del. and *Polycarpon succulentum*, Webb et Berth. (in the latter only in the neighbourhood of the leaf-margin). The cuticle is either smooth or coarsely (*Drypis*) or finely (*Gypsophila repens*, L.) punctate, or lastly striated in various ways. The **stomatal apparatus** is very characteristic, the stoma being surrounded by two subsidiary cells, which are orientated transversely to the pore. Sometimes, however, one meets with deviations from this type; in the first place, in those species in which the epidermal cells are elongated. Here the breadth of the epidermal cells, which are applied to the ends of the guard-cells, is not, so to speak, sufficient to enable these cells to clasp the guard-cells laterally as well, and in consequence of this a third and fourth epidermal cell border on the stoma on the right and left of it (*Stellaria Holostea, Cerastium hirsutum*, Ten., *Arenaria longifolia*). A second deviation from the general type and an approximation to the Cruciferous type is due to the fact that the guard-cells, instead of being suspended in the middle of the U-shaped transverse wall, are shifted along the one or the other longitudinal wall of the two subsidiary cells (i.e. one

[1] Most important literature: Vesque, 1883, loc. cit.

of the walls parallel to the pore). Thus, besides the two subsidiary cells proper, a third epidermal cell forms part of the circumference of the guard-cells. The stomata are found either on both sides of the leaf or only on the lower side; the former case holds good for leaves of centric structure, the latter for bifacial leaves. The smaller **veins** of the leaf are, as a rule, embedded in the mesophyll. Sclerenchyma accompanying the vascular bundles is only rarely developed (midrib of *Sagina Villarsii*, larger veins of *Caryophyllus plumarius*, &c.). In *Honckeneya peploides*, Ehrh. a starch-sheath has been observed in the veins; in *Agrostemma* and in *Silene fruticosa* collenchymatous differentiation of the softbast is found.

Oxalate of lime is usually present (in the axis as well) in the form of clustered crystals. These are often of considerable size. In the pith and outer cortex of the branch of *Acanthophyllum mucronatum*, C. A. Mey., I have met with

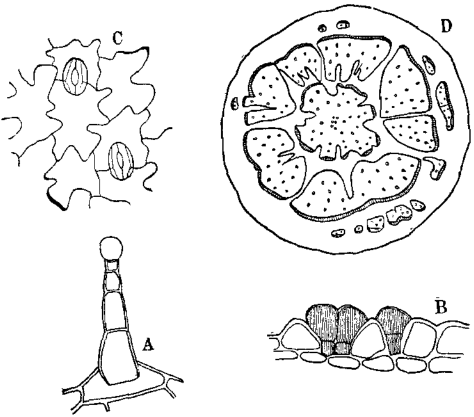

FIG. 25. A, Glandular hair of *Silene villosa*, Forsk. B, Transverse section through the outermost part of the sticky region of the stem of *Viscaria vulgaris*, Rochl. C, Epidermis of the leaf with stomata in *Viscaria vulgaris*, Rochl. D, Transverse section through the root of *Polycarpaea fragilis*, Delile.—Original.

finely divided crystal-sand consisting of oxalate of lime, which fills large tracts of the tissues named and often envelops clustered crystals. In connexion with this, the occurrence of round or angular crystalloids in the chloroplasts of the mesophyll of *Lychnis Viscaria* may be mentioned (Zimmermann).

The **hairy covering** consists of uniseriate clothing hairs and glandular hairs. The clothing hairs have a thin (*Malachium aquaticum*) or a fairly thick (*Stellaria media*, L.) wall, the surface of which may be smooth, granulated, or striate. The form of these hairs is cylindrical or conical, and their ends are pointed or rarely blunt. The individual cells of the hair are usually of equal length; *Agrostemma*, however, has hairs with short basal cells and one or several long end-cells. The uniseriate trichomes in question cause the roughnesses on the midrib and the leaf-margin of some members of the Order (species of *Arenaria*, *Cerastium*, *Stellaria*). In *Gypsophila acutifolia*, Fisch., and *Dianthus pruinosus*,

Janka, the clothing hairs are reduced to short unicellular papillae. As has already been stated, the glandular hairs are likewise uniseriate, and possess a glandular terminal cell. They have hitherto been little investigated. *Gypsophila perfoliata*, L., and *Silene villosa*, Forsk. (Fig. 25, *A*), have glandular hairs with a long, uniseriate stalk and a spherical terminal cell. Shorter glandular hairs, which have only one stalk-cell, project only slightly above the surface of the epidermis, and are associated in groups, form the well-known glandular zones of the stem in *Lychnis Viscaria* (Fig. 25, *B*). In other Sileneae, e.g. *Silene nemoralis*, the glandular zones of the stem, according to Unger, are not formed by glandular hairs but by special epidermal cells, characterized by granular contents and sometimes strongly arched outwards. Lastly, in the Caryophylleae secretion frequently also occurs in the leaf-teeth of young leaves, e.g. in *Lychnis violacea*, according to Reinke. In the example named the leaf-tooth contains a group of small-celled and pale-coloured parenchyma, together with the termination of a vein, and above this, on the upper side of the tooth, we find a number of stomata.

3. STRUCTURE OF THE STEM [1]. In the structure of the stem, the presence of a strengthening ring in the **cortex** is especially characteristic for the majority of the genera as shown by the concordant investigations of Vuillemin, K. Christ, and Petersen.

This ring, when most completely differentiated, consists of much-elongated sclerenchyma in the outer, and of sclerotic parenchyma in the inner zone. This differentiation, according to Christ, occurs in the strengthening ring in almost all the Sileneae investigated by him (species of the genera *Lychnis*, *Agrostemma*, *Silene*, *Cucubalus*, *Dianthus*, *Gypsophila*, *Saponaria*, *Velezia*) and in one group of the Alsineae (species of the genera *Holosteum*, *Cerastium*, *Moenchia*, *Moehringia*, *Alsine*, *Arenaria*, *Spergula*, *Lepigonum*, *Minnartia*, *Buffonia*). In a second group of the Alsineae, two representatives of the tribe Polycarpeae, and some few Sileneae, the inner sclerotic parenchyma of the strengthening ring is not developed; the latter is then only represented by a cylinder of tissue resembling hard bast (species of *Sagina*, *Polycarpon*, *Ortegia*, *Silene*; e.g. *S. vallesiaca*, *S. pendula*, and *S. Saxifraga*; *Lychnis*, e.g. *L. pyrenaica*; also species of *Polycarpon*, and *Polycarpaea*, according to Volkens). Lastly, in a third group of the Alsineae, in *Drymaria*, belonging to the tribe Polycarpeae, and in some few Sileneae, to make use of Christ's words in order to avoid any false interpretation on my part, the primary prosenchymatous zone of the sclerenchyma-ring (the entire inner portion having disappeared) is, as it were, shifted outwards up to the epidermis, leaving behind only a scanty rudiment of the strengthening ring close to the soft bast, while at the same time the collenchymatous and the chlorophyll-containing cortical tissue become wholly or partially lignified (species of *Moehringia*, *Malachium*, *Stellaria*, *Lepyrodiclis*, *Drymaria*, *Arenaria*, *Cherleria*, *Silene sedoides*, and *S. acaulis*); according to Brick and Petersen, *Honckenya peploides* and *Drypis spinosa* also belong to this type.

With regard to the **periderm** one gathers from the researches of Douliot, that in most cases the phellogen appears on the inner side of the sclerenchymatous sheath, or in a corresponding position when the latter is wanting; e.g. in *Dianthus*, *Silene*, *Lychnis*, *Saponaria*, *Cerastium*, *Sagina*, *Stellaria*, and *Honckenya*; in the species of *Spergularia*, on the other hand, the periderm arises in the outermost cell-layer of the primary cortex.

Only a few researches on the structure of the **wood** of the woody genera have been published. The lack of distinct medullary rays is especially noteworthy, as Oliver and Régnault have duly emphasized. Besides the vessels, which have simple perforations, and the wood-prosenchyma with simple pits, thin-walled, unlignified tissue (not phloem) frequently also takes part in the formation of the xylem-mass.

The thin-walled tissue is absent in the wood of *Dianthus trifasciculatus* (Régnault). In *Arenaria rigida*, according to the same author, this tissue forms the groundwork

[1] Most important literature: Christ, 1887, loc. cit.

of the xylem, in which vessels and groups of prosenchyma are embedded. In the two species investigated by me (*Alsine Schimperi*, Hochst. and *Buffonia enervis*, Fenzl), on the other hand, the prosenchyma forms the ground-mass, and includes unlignified tissue in concentric zones as well as vessels.

Lastly, the few cases of **anomalous structure** of the **stem and root** found in the Order must be discussed: viz. the fission of the xylem-mass in the stem in species of *Acanthophyllum*, and the appearance of successive rings of bundles in the root and stem of *Spergularia* and species of *Polycarpaea*.

Oliver first observed fission of the xylem-mass in *Acanthophyllum squarrosum*, C. A. Mey., and found similar phenomena in other species. I also have met with a split xylem-mass of this kind in *A. squarrosum*, Boiss. The young axes of this species are normal in structure, and possess a normal ring of vascular bundles. Sooner or later, however (even in branches 2 mm. in diameter), splitting of the ring takes place, e.g. by means of four radial bands of parenchymatous tissue; opposite the four arcs of wood and bast thus produced (which grow in thickness in a normal manner by means of corresponding arcs of cambium), four arcs of meristem then usually arise in the pith, forming four medullary bundles, with their xylem-groups directed outwards and their phloem-groups directed inwards [1]. These likewise grow in thickness by means of a strip of cambium situated between their xylem and phloem-portions. The strips of cambium belonging to the medullary vascular bundles finally become united at their margins with the cambium-arcs of the four bundles of wood and bast derived by splitting from the peripheral bundle-ring, so that practically four cylinders of wood and bast arise. The anomaly which occurs in *Acanthophyllum squarrosum* has also been described by Dangeard, with a few slight modifications, in *A. spinosum*, C. A. Mey., *A. bracteatum*, Boiss., and *A. Fontanesii*, Boiss. According to Dangeard, a transverse section of the older axis of *A. spinosum* shows still further complications, the anomaly being repeated, so that a transverse section of the branch finally exhibits a still larger number of rings and bundles of wood and bast. In the species of *Acanthophyllum* which have a split xylem-mass, the xylem consists, apart from the tracheides, of unlignified tissue only, fibrous cells being absent. Some other species of *Acanthophyllum* do not possess the anomaly, but are normal in structure. In these the xylem is chiefly composed of tracheae and wood-prosenchyma. These species of *Acanthophyllum* with normal structure (of which I am acquainted with *A. mucronatum*, C. A. Mey. by personal investigation, and among which *A. crassifolium*, Boiss. and *A. versicolor*, Fisch. et Mey. must be reckoned, according to Dangeard), however, have a peculiar structural feature in the xylem-ring, the same as has already been described for the Cruciferous plant, *Vella spinosa*, Boiss. A transverse section of the stem of *A. mucronatum* shows a structure which one might take for successive rings of growth on examination with the naked eye or with a lens. And, in fact, rather broad rings of woody tissue with vessels and wood-fibres and without medullary rays alternate with narrow rings of thin-walled tissue. The latter, however, do not consist of phloem, but of unlignified parenchyma, in which are embedded numerous spiral tracheae for the most part with very small lumina, and provided with more than a single spiral band. These spiral tracheae, moreover, also occur in the species without wood-fibres but with anomalous structure, e.g. in *A. squarrosum*, but are here irregularly placed among the pitted vessels; they thus appear to be in general characteristic of the genus. Among the slight modifications, which Dangeard observed in the species with normal structure investigated by him, it need only be mentioned, that the outer rings of wood are traversed by broad parenchymatous rays in *A. crassifolium*.

Secondary rings of growth have been observed by Morot in the root of *Lepigonum marinum*, by Petersen in the root of *Lepigonum salinum*, by H. Schenck in the root and stem of *Spergularia media*, Presl, and recently by me in the root of *Polycarpaea fragilis*, Del. (Fig. 25, *D*), and *P. corymbosa*, Lam. They arise extra-fascicularly.

Literature: Oliver, Struct. of the stem in cert. spec. of the nat. ord. Caryophylleae etc., Transact. Linn. Soc., vol. xxii, 4, 1859, pp. 289–94 and Pl. l, li.—Régnault, Ann. sc. nat., sér. 4, t. xiv, 1860,

[1] Sometimes (in the same species) these medullary bundles are already present before the occurrence of the splitting.

pp. 118–26, pl. vi, vii.—Delbrouck, Pflanzenstach., Hanstein, Bot. Abh., Bd. ii, 1875, pp. 28, 29.—De Bary, Vergl. Anat., 1877.—Areschoug, Bladets anat., Minnesskr., Lund, 1878, p. 73 et seq.—Vesque, Hist. Syst., Ann. sc. nat., sér. 6, t. xv, 1883, p. 130 et seq. and pl. vii.—Heinricher, Pringsheim Jahrb., Bd. xv, 1884, pp. 537–40.—Vuillemin, Péricycle des C., Bull. Soc. bot. de France 1885, pp. 275–82.—Morot, Péricycle, Ann. sc. nat., sér. 6, t. xx, 1885, p. 240.—Solereder, Holzstr., 1885, p. 147.—Christ, Vergl. Anat. des Laubst. der C. und Saxifrageen, Diss., Marburg, 1887, 83 pp. and Tab.—Lohrer, Wurzeln, Wigand, Bot. Hefte, ii, 1887, pp. 25, 26.—Volkens, Aegypt.-arab. Wüste, 1887, pp. 102, 103, 105, Taf. ii, iii, x and xv.—Brick, Schrift. Danziger naturf. Gesellsch. 1888, separate copy, pp. 30–2.—Petersen, Moment. til Caryophyll. anatomi, Botanik Tidsskrift, Bd. 16, 1888, pp. 187–202, Tab. 3, French *résumé*, p. 8.—Dangeard, Rech. de morph. et d'anat. végét., Le Botaniste 1889, pp. 194–205 and pl. ix.—Douliot, Périderme, Ann. sc. nat., sér. 7, t. x, 1889, p. 347.—Pax, in Natürl. Pflanzenfam., iii, Teil, Abt. 1 b, 1889, p. 62.—Warming, Vidensk. Meddel. naturh. For. i Copenhagen, 1890, p. 223.—Strasburger, Bau u. Verr., 1891, p. 337.—Zimmermann, Pflanzenzelle, 2. Heft, 1891, p. 150.—Warming, Meddel. naturh. Forening i Copenhagen, 1891, p. 161.—Macfarlane, Minute struct. of hybrids, Transact. Roy. Soc. of Edinburgh 1892, p. 220 et seq. and pl. iv.—Herbst, Markstrahlen, Bot. Centralbl. 1894, i, p. 297.—Russell, Ann. sc. nat., sér. 8, t. i, 1895, p. 331.—Grevillius, Engler, Bot. Jahrb., Bd. xxiii, 1896, p. 95.—Warming, Halofyt Stud., K. Danske Vid. Selsk. Skr. 1897, pp. 189, 192, 197 and 207.

PORTULACEAE.

As characteristic features of the Order from the anatomical stand-point, stress must be laid on: the simple perforations of the vessels; the simple pitting of the wood-prosenchyma; the frequent occurrence in the stomatal apparatus of two subsidiary cells placed parallel to the pore (Fig. 26, *B*); the equally frequent occurrence of mucilage-cells in the parenchyma of leaf and stem. Oxalate of lime is excreted in the form of clustered crystals, of solitary crystals, and also (*Calandrinia*) of a particular kind of sand, formed of small acicular crystals. The hairy covering consists of simple unicellular hairs, multiseriate shaggy hairs (species of *Calandrinia*, Fig. 26, *C*, and *Portulaca*), and of uniseriate glandular hairs (*Calandrinia*, Fig. 26, *D*).

The anatomical features of the Order have recently been thoroughly investigated by Becker, the investigation extendiug to twelve [1] of the eighteen genera. The following statements are derived from this source and from the remaining literature cited below.

The succulent leaves have a thick and fleshy **mesophyll**, which varies greatly in its structure. In many cases palisade and spongy tissue can be distinguished. In other cases the mesophyll is differentiated into green assimilatory cells and cells with large lumina which are almost free from chlorophyll and serve for storage of water. These two forms of cells either occur intermingled, or are localized in separate zones. In the mesophyll of *Portulaca hirsutissima*, Camb., and likewise in the primary cortex of *Portulacaria afra*, Jacq., the green cells form a network between the large, colourless cells. In *Portulaca tuberosa*, Roxb., on the other hand, the green parenchyma is found on both sides adjacent to the epidermal layer, while the middle of the leaf is occupied by colourless large-celled parenchyma. Lastly, in *Portulaca oleracea*, L. (Fig. 26, *A*), the whole mesophyll consists almost solely of aqueous tissue; the vascular bundles only are surrounded by a sheath of green palisade-parenchyma. Under certain circumstances the localization of aqueous cells amongst the green leaf-tissue may in the dry leaf lead to the appearance of transparent regions, as described by Blenk in certain species of *Portulaca*. The **stomata** always occur on both surfaces of the leaf. In most cases (species of all the genera investigated by Becker excluding *Calandrinia* and *Montia*) the stomata [2]

[1] Namely: *Portulaca*, *Portulacaria*, *Anacampseros*, *Talinum*, *Calandrinia*, *Claytonia*, *Spraguea*, *Monocosmia*, *Montia*, *Hectorella*, *Calyptridium*, *Lewisia*.

[2] The stomatal apparatus in this case arises only in some cases, e.g. in *Portulaca*, according to the Rubiaceous type. In *Claytonia perfoliata* the subsidiary cells do not proceed from the

are accompanied on both sides by a subsidiary cell placed parallel to the pore (Fig. 26, *B*). In *Calandrinia* the stoma is surrounded by four subsidiary cells, as in *Tradescantia*; in *Montia* true subsidiary cells are absent. The **veins**, as far as is known, are embedded in the mesophyll and are without sclerenchyma. **Oxalate of lime** occurs in three forms, as clustered crystals, as solitary crystals (which, according to Becker, belong to the tetragonal system), and as crystal-sand. In the leaf, Becker observed clustered crystals alone in *Calyptridium*, *Lewisia*, *Monocosmia*, *Portulaca*, *Portulacaria*, and *Talinum*, clustered crystals and solitary crystals in *Anacampseros* and *Spraguea*, and a peculiar crystal-sand, consisting, according to my own investigation, of small needles and small prismatic crystals, in *Calandrinia*. At the same time it may be added, that in the stem oxalate of lime is met with in the form of clustered crystals. *Claytonia* and *Montia* have no deposits of oxalate of lime either in leaf or stem. Of internal **secretory elements**, mucilage-cells alone occur in the Order. These take part in the storage of water, and, among the genera investigated by Becker, are wanting only in *Montia* and *Claytonia*. They are met with in the leaf-tissue as well as in the ground-tissue of the stem, and are sometimes (*Anacampseros* and *Portulacaria*) of considerable size. The contents of the mucilage-cells in question are membrane-mucilage, according to Walliczek; further detailed investigations regarding this point are, however, desirable. In view of such investigations it may be remarked that, according to Becker, the mucilage-cells arise very early. A **hairy covering** is not common in the Order. It consists (when present) (*a*) of simple, unicellular, thin-walled hairs, rounded at the apex, and with smooth or granular surface (species of *Calandrinia* and *Portulaca*), (*b*) of multiseriate shaggy hairs, the superficial cells of which (elongated in the direction of the length of the hair) may or may not project as papillae (*Calandrinia umbellata*, Fig. 26, *C*, *C. pilosiuscula*, and *Portulaca pilosa*), and (*c*) of uniseriate short-celled glandular hairs (*Calandrinia umbellata*, Fig. 26, *D*). In connexion with these hair-structures we may mention the bladder-like protrusions of single epidermal cells occurring on the stem and leaf in *Talinum* and *Spraguea*, forming a transition to the hairs, and apparently serving for water-storage.

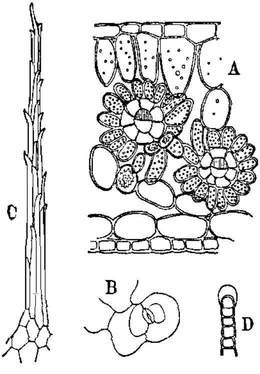

FIG. 26. A, Transverse section of the leaf of *Portulaca oleracea*. B, Stomatal apparatus of *Portulaca oleracea*. C, Shaggy hair, and D, Glandular hair of *Calandrinia umbellata*.—After Vesque.

Regarding the **xylem-mass**, what has already been said above should be repeated, namely, that the vessels have simple perforations and that the wood-fibres, when they occur, are always simply-pitted. Becker, extending the statements in my 'Holzstruktur,' has also met with these two features in the comprehensive material investigated by him. The differentiation of the vascular system in the stem varies greatly in its more special details.

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original mother-cell of the pair of guard-cells, but from cells adjoining it (Strasburger, Pringsheim Jahrb., Bd. v, 1866-7, p. 326 and Taf. xl).

In *Portulacaria afra*, Jacq., the vascular bundles are separated from one another by broad unlignified medullary rays; the xylem of the former consists of wood-prosenchyma with simple pits and of tangential bands of unlignified thin-walled cells, including pitted vessels, which have delicate spiral or reticulate thickenings. According to Régnault, a plant described as *Talinum speciosum*, and also *T. fruticosum*, have similar features. In both of these plants isolated bundles of bast-fibres are present in the pericycle. Most of the investigated species of *Portulaca*, e.g. *P. grandiflora*, exhibit an essentially different type. In these plants the xylem, apart from the primary groups of vessels which project into the pith, consists of a prosenchymatous strengthening ring, which contains but few vessels and no medullary rays. In still other Portulaceae this ring of wood is wanting; the vascular bundles remain isolated; as a substitute for the intracambial strengthening ring, an extracambial zone occurs in the pericycle of these species in the form of a ring of bast-fibres. To this type, according to Becker, belong species of *Calandrinia, Calyptridium, Lewisia* (flower-stalk), *Monocosmia, Spraguea*, and *Talinum*. Lastly, in *Anacampseros, Claytonia*, and *Montia*, the vascular bundles likewise remain isolated; in these, however, neither the intracambial nor the extracambial strengthening ring is present.

Special mention should also be made of the occurrence of numerous short spindle-shaped, spiral tracheides in the pith of the species of *Anacampseros* (*A. arachnoides*, and *A. filamentosa*) investigated by Becker.

¹Literature: Régnault, Anat. de qu. tiges des Cyclospermées, Ann. sc. nat., sér. 4, t. xiv, 1860, pp. 106–12 and pl. vi.—Vesque, Hist. syst. de la feuille des Caryophyllinées, Ann. sc. nat., sér. 6, t. xv, 1883, pp. 134–6 and pl. vii.—Blenk, Flora 1884, p. 110, separate copy, p. 24.—Solereder, Holzstr., 1885, pp. 73, 74.—Christ, Vergl. Anat. Laubst. d. Caryophyllinen etc., Diss., Marburg, 1887, pp. 68–71.—Lohrer, Wigand, Bot. Hefte, ii, 1887, pp. 27, 28.—Pax, in Natürl. Pflanzenfam., iii. Teil, Abt. 1 b, 1889, p. 52.—Benecke, Nebenz. d. Spaltöffn., Bot. Zeit. 1892, p. 577 et seq.—[Rogger, Stud. anat. sulla *Portulaca oleracea*, Treviso, 1892.]—Walliczek, Membranschleime, Pringsheim Jahrb., Bd. xxv, 1893, p. 213.—Becker, Vergl. Anat. d. P., Diss., Erlangen, 1895, 38 pp. and 3 Tab.—Schubert, Parenchymscheiden, Bot. Centralbl. 1897, iii, p. 343.—Warming, Halofyt Stud., K. Danske Vid. Selsk. Skr. 1897, p. 223.

TAMARISCINEAE.

1. Review of the Anatomical Features. Almost all the Tamariscineae have small, often scale-like leaves, and in correspondence with this exhibit (with the exception of *Fouquiera*) centric leaf-structure. Stomata almost always occur on both surfaces of the leaf. The guard-cells are not accompanied by any special subsidiary cells. It is a striking feature in the species of *Tamarix, Myricaria, Hololachne*, and *Reaumuria*, that the pores of the stomata on the leaves are placed transversely to the course of the veins. The hairy covering consists of simple unicellular hairs; together with these there occur external glands of characteristic structure identical with those of the allied Frankeniaceae (cf. Fig. 24). These glands are not hair-like; they consist of a four-celled glandular group and of two subsidiary cells, and have been observed in all the genera except *Fouquiera*. Oxalate of lime is deposited in the form of clustered and solitary crystals or is absent. The vessels of the wood have, for the most part, simple perforations. The development of the cork is superficial (*Tamarix*) or internal (*Reaumuria*).

The following features can be made use of for specific and generic diagnosis respectively: for the former, the papillose nature of the epidermis (species of *Reaumuria* and *Tamarix*), the occurrence of sclerenchyma in the veins, of sclerenchyma-fibres (*Reaumuria oxiana*, Boiss.) and storage-tracheides (species of *Tamarix* and *Reaumuria*) in the mesophyll; for generic diagnosis, the presence or absence (*Reaumuria*) of medullary rays, the nature of the pitting of the wood-prosenchyma (bordered pits in *Fouquiera*, simple pits in *Reaumuria* and *Tamarix*), the size of the bordered pits on the walls of the vessels, the septation of the pith without sclerosis (*Fouquiera*).

2. Structure of the Leaf[1]. In most of the genera, namely, those which have small scale-like leaves, the **mesophyll** is centric in structure (*Tamarix, Myricaria, Hololachne,* and *Reaumuria*). An exception to this is afforded by *Fouquiera* only, which has flat broad leaves and normal bifacial structure, as well as by those species of *Tamarix* with an abortive lamina, e.g. *Tamarix articulata,* Vahl and *T. dioica,* Roxb., in which palisade-parenchyma is developed only on the (lower) side of the leaf-sheath, which is turned towards the light. The **epidermal cells** on both surfaces of the leaves have straight lateral walls. In *Tamarix gallica,* L. and *T. deserti,* Boiss. the epidermal cells on the upper side of the leaf are produced into more or less elongated papillae; in *Reaumuria hirtella,* Jaub. et Spach, the epidermal cells on both sides of the leaf are bulged outwards at the middle into knob-like papillae; lastly, in *Myricaria germanica* the outer walls of the epidermal cells of both sides are arched outwards, almost forming papillae on the lower side. The cuticle varies in thickness, and is smooth, striate, or punctate; sometimes wax is deposited on it (*Reaumuria hirtella,* Jaub. et Spach). In all the members of the Order, with the exception of *Myricaria germanica* and the species of *Tamarix* with an abortive lamina, **stomata** are present on both sides of the leaf, although in *Fouquiera* they are less numerous on the upper side. The pair of guard-cells is as a rule surrounded by several epidermal cells, of which two are sometimes (*Myricaria germanica*) placed parallel to the pore. It is a very noteworthy fact that the pore of the stoma is frequently placed at right angles to the course of the vein (in *Tamarix, Myricaria, Hololachne, Reaumuria,* but not in *Fouquiera*); an analogous arrangement of the stomata also occurs in the branch (*Tamarix* according to Volkens). In the genus *Reaumuria,* however, in which the guard-cells are always strongly depressed below the level of the surface of the leaf, the direction of the pore is sometimes irregular. The **veins** are always embedded in the mesophyll, the middle region of which is sometimes differentiated as aqueous tissue (*Reaumuria hirtella*). **Sclerenchyma** accompanying the vascular bundles is as a rule absent, but is sometimes developed as rather stout strands in some species of *Tamarix,* e.g. *T. octandra,* Bunge. The aqueous tissue occupying the middle of the leaf of *Hololachne songarica,* Ehrenb., becomes sclerotic in the peripherally situated parts. *Reaumuria* (*Eichwaldia*) *oxiana,* Boiss. possesses irregularly branched sclerenchyma-fibres, which run free in the mesophyll. Lastly, storage-tracheides occur in the leaf-tissue in certain species of *Tamarix* and *Reaumuria* (in *T. articulata,* Vahl and *T. mannifera,* Bunge; further, in *R. hypericoides,* Willd. var. *latifolia,* Trautv., *R. hyrcanica,* Jaub. et Sp., *R. mucronata,* Jaub. et Sp., *R. oxiana,* Boiss., *R. squarrosa,* Jaub. et Sp., *R. stenophylla,* Jaub. et Sp., where they are restricted to the middle zone of the leaf; lastly, in *R. persica,* Boiss. and *R. filifolia,* Jaub. et Spach, scattered through the entire mesophyll). These storage-tracheides apparently also have a mechanical function, for they frequently grow to an extraordinary extent and project between the palisade-cells up to the epidermis of the leaf.

Oxalate of lime is present in the form of clustered or rarely of solitary crystals (*Tamarix, Reaumuria*). In *Hololachne, Myricaria,* and *Fouquiera* crystals have not been observed. True **internal glands** are absent; gelatinization of the epidermis has likewise not been observed in this Order. According to Volkens the abundance of tannin in the palisade-tissue is noteworthy.

With regard to the **hairy covering,** simple, unicellular hairs with thick

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[1] Principally according to Vesque, Ann. sc. nat., 1883, loc. cit. Numerous species of all the genera (*Tamarix, Myricaria, Hololachne, Reaumuria* and *Fouquiera*) were investigated by Vesque. The work contains synopses of the anatomical structure of the leaf in the different species of *Tamarix* and *Reaumuria.*

walls and narrow lumina are found in species of *Reaumuria* and in *Myricaria germanica*; *Fouquiera* also has simple unicellular hairs with blunt apices. Moreover, external glands of extremely characteristic structure occur in all species hitherto investigated of *Tamarix*, *Myricaria*, *Hololachne*, and *Reaumuria*, but not in *Fouquiera*. According to Volkens' description in *Reaumuria hirtella*, Jaub. et Spach, they consist of a spherical structure, which does not project as a hair, and is divided by a wall perpendicular and by one approximately parallel to the external surface of the leaf into four thin-walled cells of about equal size, and having a secretory function; towards the interior of the leaf two subsidiary cells are attached to the lower pair of glandular cells; these subsidiary cells result from the displacement and depression of epidermal cells. The glands are usually strongly depressed in the surface of the leaf and cause the 'folia impresso-punctata'[1] of systematists. As to whether the structure, described by Volkens in *Reaumuria hirtella* and figured in *Tamarix mannifera*, Vahl, applies to all the glands of this Order, requires further investigation; for Vuillemin describes the glands of the Tamariscineae as similar to those of the Frankeniaceae and, in agreement with this, states that they consist of only one pair of secretory cells and of two subsidiary cells; this, however, according to my own researches, proves not to be true, or at least not generally so, and this statement applies to both Orders. It may be remarked with regard to the physiological significance of these glands that the pits (often of considerable depth), at the base of which they are found, are filled with secreted hygroscopic salts (common salt, and also carbonate of lime), which subsequently, during the dry season, attract the moisture present in the air in the vaporous form and supply it to the plant through the glands. In agreement with this the palisade-cells in the neighbourhood of the glands are frequently applied to the glandular apparatus, the peripheral cells having curved tips.

3. STRUCTURE OF THE BRANCH. The following facts may be mentioned regarding the structure of the **wood** in the three more closely investigated species, *Tamarix gallica*, L., *Reaumuria hypericoides*, Willd. var. and *Fouquiera splendens*, Engelm. *Fouquiera* and *Tamarix* have 4–5-seriate medullary rays, while in *Reaumuria* medullary ray-parenchyma is absent. The vessels bear bordered pits of variable size on their walls; they are small in *Tamarix* (diameter of the border $= 3\ \mu$), and relatively large ($6\ \mu$) in *Fouquiera*. In *Tamarix* bordered pits occur on the vessel-wall where it is in contact with the parenchyma of the medullary rays; in *Fouquiera* transitions from bordered to simple pits occur. The perforations of the vessels are simple, circular or elliptical, in *Fouquiera* sometimes elongated-elliptical, or even scalariform with few bars. The wood-prosenchyma has simple pits in *Tamarix* and *Reaumuria*; in *Fouquiera* it has distinct, but not abundant, bordered pits. The **pith** of *Fouquiera splendens* is septate without sclerosis, in the same manner as in the genus *Carya* of the Juglandeae; the same applies to *F. formosa*, H. B. K.

Möller gives the following description of the structure of the **cortex**, founded on an investigation of *Tamarix gallica*, L. The periderm arises superficially beneath the epidermis and consists of small thick-walled cells. The primary cortex has no collenchyma, is devoid of crystals, and only contains isolated enlarged stone-cells. The pericycle is composed of extensive bundles of primary bast-fibres, which are in mutual contact at the time of their origin, but afterwards move apart from one another, without any sclerosis taking place in the parenchyma which becomes inserted between them. In the secondary bast, bast-fibres, appearing in the form of massive strands, which are convex towards the exterior, take up the entire breadth of the bast-ray, and are tangentially seriated. Between the bundles of bast-fibres of the

[1] The interpretation of these dots by Blenk is very incomplete.

secondary bast the cells of the broad medullary rays become sclerotic to a slight extent and contain ordinary solitary crystals. The sieve-tubes have simple sieve-plates. Lastly, with regard to the cortex of *Reaumuria hirtella* we may quote Volkens' statements that in this plant the whole of the primary cortex consists of colourless, water-storing tissue, and that internal formation of cork takes place.

· Literature: Möller, Holzanat., Denkschr. Wiener Akad. 1876, p. 83 and 379.—De Bary, Vergl. Anat., 1877.—Möller, Rindenanat., 1882, pp. 254, 255.—Vesque, Feuille des Caryophyllinées, Ann. sc. nat., sér. 6, t. xv, 1883, pp. 137–47 and pl. viii.—Blenk, Flora, 1884, p. 110, separate copy, pp. 24, 25.—Solereder, Holzstr., 1885, p. 74.—Volkens, Sitz.-Ber. Berliner Akad. 1886, vi, separate copy, p. 8 et seq.—Marloth, Ber. deutsch. bot. Gesellsch. 1887, p. 319 et seq.—Volkens, Aegypt.-arab. Wüste, 1887, pp. 106–8 and Taf. v.—Vuillemin, Ann. sc. nat., sér. 7, t. v, 1887, pp. 173, 174 and pl. iv.—Niedenzu, in Naturl. Pflanzenfam., iii. Teil, Abt. 6, 1895, p. 290.—Warming, Halofyt Stud., K. Danske Vid. Selsk. Skr. 1897, p. 216.

ELATINEAE.

We owe our information regarding the anatomy of this small Order, which consists only of the two genera *Bergia* and *Elatine*, chiefly to the recent statements of Niedenzu.

Immediately below the 2–3 epidermal layers, from which the trichomes arise, the stem-structure of the terrestrial species of *Bergia*, according to Niedenzu, shows a many-layered starch-sheath, which is specially well developed in *Bergia glomerata*, L. f. Internal to this lies the cortical parenchyma which, like the pith, contains clustered crystals; isolated groups of hard bast form the outer limit of the bast. Some other species of *Bergia* and the genus *Elatine* present different features in the structure of the cortex. Even in *Bergia anagalloides*, E. Mey. and *B. arenarioides*, Fenzl, large intercellular spaces are found in the inner part of the primary cortex; in *B. aquatica*, Roxb. and in all the species of *Elatine*, in conformity with their amphibious mode of life, one finds wide vertical air-passages, which are separated from one another by one-layered, radial, parenchymatous plates consisting of cells which are usually radially elongated; it may be added that these air-passages recur in the primary cortex of the root, where they are traversed by radial filaments of parenchymatous cells. Hard bast is absent from the pericycle in *Elatine*, as also in some species of *Bergia*; in place of it there is an endodermis with suberized, radial walls. In the species of *Elatine* the pith is also generally (with the exception of *E. Alsinastrum*, L.) absent.

Regarding the nature of the **wood** of *Bergia suffruticosa*, Fenzl, a woody species, I have pointed out the following facts in my 'Holzstruktur.' The medullary rays of the wood are at the most qnadriseriate; their cells are elongated in the vertical direction. The vessels lie scattered in the transverse section, are four-sided and have simple elliptical or circular perforations as well as bordered pits even on the parts of the wall which border on parenchyma of the medullary rays. Wood-parenchyma is little developed; the wood-prosenchyma has moderately thick walls and bordered pits. In contradistinction to this the woody tissue in *Elatine*, according to F. Müller and H. Schenck, is composed entirely of vessels and thin-walled wood-parenchyma. Niedenzu describes more or less quadrangular vessels with simple perforations as being quite general in the Elatineae.

The following facts should be cited, for the most part from Niedenzu, regarding the structure of the leaf, the hairy covering and the occurrence of secretion in the Order. The **epidermis** of the leaf usually consists of very large cells, and often contains, e.g. in *Bergia decumbens*, Planch., special large water-storing cells, which are arched outwards above the surface of the leaf and are some-

times visible in the living plant, even with a lens, as shining dots. In the veins hard bast is usually absent. In the two species investigated by me (*Bergia texana*, Seub., and *Elatine Alsinastrum*, L.) the **stomata** are surrounded by several ordinary epidermal cells. Mucilaginous epidermal cells are present in *Bergia texana*.

The **hairy covering** consists of clothing and glandular hairs. The clothing hairs in *Bergia suffruticosa*, *B. arenarioides* and others have a conical form and are 1–2-celled; they cover the whole plant in abundance. Niedenzu also met with multicellular, uniseriate clothing hairs in *B. arenarioides*; they are segmented in such a way that ventricose and slender cells alternate. The glandular hairs are of the shaggy form, with a multiseriate stalk and a multicellular head. They form the terminations of the leaf-teeth, and are found on the lower side of the ribs of the leaf, but also elsewhere on the leaf and stem.

Respecting the occurrence of **secretions** I quote Niedenzu's statements verbally. In several species of *Bergia* (e.g. *B. arenarioides*, *B. ammanioides*, Roxb., *B. polyantha*, Sond, and others) a secretion occurs, which is brownish in the dry condition and is probably resinous; it is found in the parenchymatous cells, in the epidermal cells, and in the leptom-cells of the stem and in the leaves (especially in the vascular bundles); it is embedded in a pseudo-cellular matrix in the cells of *B. arenarioides*; in *B. decumbens*, Planch., it is excreted in distinct granules, visible to the naked eye and deposited on the surface of the stem, and is the cause of the camomile-smell, to which *B. suffruticosa* owes the synonym *B. odorata*, Edgew.

Literature: F. Müller, Strukt. einig. A. von Elatine, Flora 1877, p. 481 and 519, Tab. iii.—Areschoug, Blad. anat., Minesskrift, Lund, 1878, p. 141 et seq. and Tab. ix.—Solereder, Holzstr., 1885, p. 75.—H. Schenck, Vergl. Anat. d. submers. Gew., Bibl. bot., Heft 1, 1886, p. 33 and Taf. v.—Niedenzu, in Natürl. Pflanzenfam., iii. Teil, Abt. 6, 1895, p. 278.

HYPERICINEAE.

1. Review of the Anatomical Features. Noteworthy features in all the members of the Order are the occurrence of schizogenous secretory cavities in *the leaf, frequently causing transparent or black, opaque dots, and the occurrence of schizogenous secretory canals in the bast of the axis*. In the axis of certain species the secretory canals sometimes occur also in the pith, pericycle, and primary cortex, but the secretory cavities are only very rarely found here (in the primary cortex). The axis is further characterized by the presence of a ring (often closed) of sclerenchyma-fibres in the pericycle of the woody species; by narrow medullary rays in the wood; by vessels with simple perforations; by wood-prosenchyma with simple or with slightly bordered pits; as well as by internal, never superficial, formation of cork. In *Hypericum*, the stomata are surrounded by three epidermal cells; in the Vismieae and Cratoxyleae they are accompanied by two subsidiary cells, which are parallel to the pore. Stellate hairs with uniseriate stalks are found in *Vismia*, *Psorospermum* and *Haronga*; glandular hairs have not been observed. Oxalate of lime is excreted in the form of clustered crystals, in the axis also in the form of solitary crystals. The following are special anatomical features which may be utilized either for generic or specific diagnosis: the abundant development of wood-parenchyma in the form of tangential bands in the xylem-mass of some genera; the papillose differentiation of the lower epidermis of the leaf (species of *Vismia* and *Psorospermum*); the development of hypoderm on the upper side of the leaf (species of *Vismia*) and of storage-tracheides in the mesophyll (*Endodesmia*).

2. Structure of the Leaf[1]. The **mesophyll**, so far as is known, is bifacial in structure. The numerous species of *Vismia* and *Psorospermum* investigated by Vesque all have a one-layered palisade-tissue, the cells of which are very much elongated in the species of the first-named genus but not in those of the second (*Psorospermum*). Papillose differentiation of the lower **epidermis** of the leaf is described in *Vismia latifolia*, Choisy, and *Psorospermum discolor*, Spach. A 1-3-layered **hypoderm** occurs on the upper side of the leaf in numerous species of *Vismia* (in *V. cayennensis*, Pers., *V. eriantha*, Mart., *V. glabra*, Ruiz et Pav., *V. lasiantha*, Klotzsch, *V. lauriformis*, Choisy, *V. reticulata*, Choisy, *V. rufescens*, Pers., *V. sessilifolia*, Pers.). The **stomata** are only present on the lower side of the leaf. According to Vesque the two guard-cells are surrounded by three epidermal cells in *Hypericum*, but in the Cratoxyleae and Vismieae they are accompanied by two subsidiary cells parallel to the pore. With regard to the structure of the **veins** in *Vismia*, Vesque states that a mass of sclerenchyma is placed above and below the vascular bundles. Lastly, the presence of storage-tracheides in the leaf-tissue recorded in the case of *Endodesmia*.

Secretory cavities[2] are found in the leaves of all the genera, as we know chiefly from the work of Blenk and Van Tieghem, the latter of whom also investigated the two genera *Eliaea* and *Endodesmia*, which were not accessible to Blenk. According to the concordant researches of Frank, Höhnel, Wieler, Blenk, Kienast, and Leblois, the origin of these secretory cavities is schizogenous, and not lysigenous, as Martinet, Chatin, De Bary, and Green supposed. It is a well-known fact that the secretory cavities of this Order frequently cause transparent dots in the leaves; and that black opaque dots, likewise caused by secretory cavities, but limited to the genus *Hypericum*, occur, either accompanying the transparent dots, or rarely to the exclusion of the latter; these secretory cavities, however, are filled with dark contents, and are either restricted to the margin of the leaf, or occur also on the surface of the leaf. The secretory canals of the petiole will be discussed later in connexion with the secretory canals of the axis.

Oxalate of lime is contained in the leaf-tissue in the form of clustered crystals in *Vismia*, *Psorospermum*, and *Haronga*, according to Vesque.

With regard to the **hairy covering**, Vesque mentions the occurrence of stellate hairs with a uniseriate stalk in the three genera just mentioned. In *Vismia laurifolia*, Choisy, the ray-cells of these stellate hairs are so firmly interwoven with one another, that the species in question, in spite of the abundant hairy covering on the lower surface of the leaf, was described as glabrous. Glandular hairs have not been observed. The varnish-like covering of the leaf of *Hypericum resinosum*, Benth., is caused, according to Volkens, not by glandular hairs, but in all probability by the secretory cavities.

3. Structure of the Axis. Regarding the structure of the **wood** in this Order, investigations of the genera *Hypericum* (Turner and Solereder), *Ancistrolobus* (Möller), and of *Ascyrum*, *Vismia*, *Psorospermum*, *Cratoxylon*, and *Tridesmis* (Solereder) have been published. In these genera narrow medullary rays always occur. The vessels, which usually lie scattered in a transverse section of the branch, have lumina of different sizes (maximum diameter, ·024 mm. in *Hypericum Buckleyi*, Curt., ·081 mm. in *Vismia baccifera*, Reich.); the division-walls of the vessels are simply-perforated. On the vessel-wall bordering the parenchyma of the medullary rays one finds bordered pits or more or less distinct simple pits, which, as a rule, are not large. The wood-parenchyma

[1] Most important literature: Vesque, 1885 and Blenk, 1884, loc. cit.

[2] The statement of Parmentier (loc. cit.) as to the occurrence of oil-cells in *Hypericum* is incorrect

is developed in the form of tangential bands in the investigated species of *Ancistrolobus, Vismia, Psorospermum, Cratoxylon,* and *Tridesmis.* The walls of the wood-prosenchyma usually have distinct, small bordered pits (*Vismia, Psorospermum, Cratoxylon, Tridesmis*) or simple pits (*Hypericum, Ascyrum*). Together with this prosenchyma bearing simple or slightly bordered pits there frequently occur prosenchymatous elements (so-called tracheides) with distinct and relatively wide-bordered pits, which form a transition to the vessels, and in *Hypericum Buckleyi,* Curtis, are spirally thickened.

As to the **cortex** it is known from Van Tieghem's statements that only thin-walled tissue is present in the pericycle in the herbaceous members of the Order (species of *Hypericum, Tridesmis, Ascyrum*); while in the woody species a ring (often closed) of sclerenchyma-fibres occurs (species of *Ancistrolobus, Cratoxylon, Eliaea, Haronga, Psorospermum, Endodesmia*) in this region. In both cases the cork arises in the pericycle, in the second case internally to the ring of sclerenchyma-fibres. Douliot makes some statements on the detailed structure of the cork. U-shaped, thickened cells occur in the cork of '*Cratoxylon coccineum,*' *Tridesmis Billardieri,* and *Eliaea articulata*; in the last-named species layers of cells thickened in this manner alternate with unthickened layers of cork-cells. Unsuberized cells have been observed in the cork of *Ascyrum Crux-Andreae, Vismia cayennensis,* and *Eliaea articulata.* Lastly, it may be added that formation of aerenchyma has been observed by H. Schenck in *Hypericum brasiliense,* Choisy.

The secretory cavities of the lamina of the leaf are replaced in the axis by schizogenous (Leblois) **secretory canals,** which were first observed by Konrad Müller, and were afterwards thoroughly investigated by Van Tieghem. It is only in rare cases that secretory cavities are also found in the branch, where they occur in the primary cortex (*Hypericum balearicum*). According to Van Tieghem the secretory canals are always present in the secondary bast of the axis. Moreover, they sometimes also occur in the pith, the pericycle and the outer part of the primary cortex, either in all three tissues or only in one of them; these diverse modes of occurrence are mostly only of specific value according to our present knowledge.

As regards the presence of secretory canals in the pericycle, they are found in that tissue in the herbaceous species only, the pericycle here consisting exclusively of parenchymatous tissue (*Hypericum, Tridesmis, Ascyrum*). On the occurrence of medullary and cortical secretory canals we have the following observations of Van Tieghem's. The secretory canals are present in the pith and primary cortex in *Hypericum calycinum, Tridesmis Billardieri, Haronga madagascariensis, Endodesmia calophylloides*; only in the primary cortex in *Hypericum Elodes, H. Androsaemum, Psorospermum senegalense*; only in the pith in *Ancistrolobus* '*pulchellus,*' and *A. ligustrinus, Eliaea articulata,* '*Cratoxylon coccineum,*' and according to K. Müller in *C. myrtifolium.* The medullary and cortical secretory canals are, on the other hand, wanting in most of the species of *Hypericum,* e.g. *H. perforatum, H. tetrapterum,* &c., further, in *Ascyrum Crux-Andreae, Vismia cayennensis,* and, according to K. Müller, also in *V. tomentosa,* Ruiz et Pav. and *V. glabra,* Ruiz et Pav. Finally, it should also be noted, that the number and arrangement of the medullary and cortical secretory canals can be made use of for specific diagnosis.

The resin-canals are also found in the petiole, while in the leaf itself they are replaced by secretory cavities (see above). In all the members of the Order the petiole possesses only a single arc-shaped vascular bundle-system. When the pericycle of the latter is parenchymatous, as in *Cratoxylon* and *Haronga,* it contains oil-canals. When the branch exhibits secretory canals in the primary cortex, these may run as far as the base of the leaf, and in the petiole may be arranged in the form of an arc on the lower side of the vascular bundle-system (*Hypericum calycinum, Haronga, Psorospermum, Tridesmis, Endodesmia*). Further, if the branch has medullary resin-canals, they may also occur in an analogous position in the petiole, viz. on the upper side of the vascular bundle-system (*Tridesmis, Endodesmia*), or they may be wanting in that position (*Hypericum calycinum, Cratoxylon, Eliaea, Haronga*).

Lastly, in *Ancistrolobus* we find that the stem has medullary but no cortical resin-canals, while in the petiole they only occur on the lower side of the vascular system.

In *Hypericum* the secretory canals are also present in the root, where they occur in the pericycle on the right and left of the phloem-bundles of the radially differentiated fibro-vascular system. In older roots one meets with them in the secondary bast also.

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GUTTIFERAE (INCL. QUIINEAE).

1. REVIEW OF THE ANATOMICAL FEATURES. The type of stomatal apparatus, i.e. the occurrence of subsidiary cells parallel to the pore on either side of the pair of guard-cells (Fig. 27, *C*), is characteristic of all the Guttiferae, as also—with the exception of the Quiineae—is the presence of schizogenous, intercellular, secretory receptacles (canals, or canals and cavities). Secretory canals are present in the pith and in the primary cortex of the axis in almost all the members of the Order; at the same time, they sometimes also occur in the primary and secondary bast, or in the secondary bast only. In the leaf the secretory canals either follow the vascular bundles in the veins or run independently of the vascular bundles in the mesophyll; in the latter case they are sometimes (in the genus *Calophyllum*, see Fig. 27, *D*) accompanied by peculiar bundles of tracheides and by sclerenchyma. In some genera the secretory canals of the leaf-tissue are in part replaced by secretory cavities (*Garcinia* pro parte, *Kayea*, *Mammea*, *Mesua*, *Ochrocarpus* pro parte, *Pentadesma*, *Poeciloneuron*). The varied distribution of the secretory canals in stem, root, and leaf is important for generic and specific diagnosis. It may also be pointed out in connexion with the description of the intercellular secretory organs, that mucilaginous epidermal cells of the leaf have not been observed in any member of the Order, but, on the other hand, lysigenous mucilage-receptacles are found in the genus *Quiina* (see below).

Among further features the occurrence of simple perforations in the vessels and of parenchymatous bands in the xylem-mass is characteristic of all the Guttiferae. The wood-prosenchyma has simple or slightly bordered pits; the medullary rays of the wood are never very broad. Oxalate of lime is deposited in the form of clustered and of ordinary solitary crystals, more rarely (in the epidermis of the leaf of species of *Garcinia* and *Tovomita*) in the form of small, mostly prismatic crystals. A hairy covering (Fig. 28) seldom

occurs in the Order; glandular hairs are completely absent; there are only simple unicellular hairs (*Garcinia*), or simple uniseriate hairs, the latter, owing to papillose protrusion of cells, passing over into branched or dichotomously divided hairs (*Calophyllum*). The nature of the vessel-wall where it is in contact with ray-parenchyma (whether bearing bordered pits or large simple pits), the varying place of origin of the cork (epidermis or outermost cell-layers of the primary cortex), and the structure of the veins (embedded or vertically transcurrent) can probably be employed for generic diagnosis. In the same way, apart from the form and distribution of the secretory organs already referred to above, and from the diverse nature of the (usually bifacial) mesophyll and the varying form of the epidermal cells, numerous anatomical characters (especially of the leaf) are available for distinguishing the species, viz.: very frequently a hypoderm; in a few species a papillose epidermis on the lower side of the leaf; in many species papillose or strongly striate subsidiary cells in the stomatal apparatus; marginal pits in the epidermal cells; sclerosed mesophyll-cells; terminal tracheides; small columnar or clustered crystals in the epidermis of the leaf; cork-warts on the lower surface of the leaf, &c.

The Quiineae (genus *Quiina*, including *Touroulia*), which are regarded by Engler as a separate Order, are essentially distinguished from the Guttiferae by the absence of schizogenous resin-canals and by the occurrence of lysigenous mucilage-canals. In regard to their remaining anatomical features the Quiineae fall into the circle of affinity of the Guttiferae.

2. Structure of the Leaf[1]. The leaf-structure is well known through the investigations of Vesque and Blenk.

The **mesophyll** is bifacial in structure in most cases. Centric or subcentric structure has been observed in certain species of *Calophyllum, Garcinia, Rheedia, Clusia, Symphonia, Moronobea, Platonia*, and *Pentadesma*. The palisade-tissue consists either of long or short cells; the spongy parenchyma is usually loose. The mesophyll of *Clusia rosca*, L., shows a very remarkable structure. In this species the palisade and spongy parenchyma are distinguished by having reticulately thickened walls; the cells of the palisade-tissue have, at the same time, nearly prosenchymatous shape (Fig. 27, *A*). In other Guttiferae there is a tendency to sclerosis in the mesophyll. Thus in many species of *Clusia* and *Cochlanthera* the whole of the lower part of the spongy tissue is thick-walled or sclerotic; in certain species of *Clusia* (*C. insignis*, Mart.), *Pilosperma* (*P. caudatum*, Tr. et Pl.), *Tovomita* (*T. macrophylla*, Walp.), *Montrouziera* (*M. cauliflora*, Tr. et Pl.) and *Poeciloneuron* (*P. indicum*, Bedd.) this feature is restricted to one or rarely two layers of cells which are situated above the lower epidermis and possibly, in part (*Clusia insignis*), also belong to the epidermal tissue; lastly, in certain species of *Clusia* (*C. volubilis*, H. B. K.) and *Garcinia* (*G. Blumei*, Pierre, *G. echinocarpa*, Thw., *G. Hasskarlii*, Pierre, *G. myristicaefolia*, Pierre, *G. picrorhiza*, Miq.) only isolated cells of the mesophyll are sclerosed.

The structure of the **epidermis** affords a whole series of anatomical characters: firstly, the varied nature of the lateral walls, which, according to the species or genus, are straight to strongly undulated; then, the height of the epidermal cells and their consequent shape in a transverse section of the leaf; the varied thickness of the cuticle; the appearance of marginal pits in epidermal cells with undulated lateral walls (in certain species of *Tovomita*,

[1] Chiefly according to the works of Vesque, 1886–93, and Blenk, 1884, loc. cit. In the following description of the leaf-structure I omit enumerations of species as far as possible, as any one who is specially interested in the anatomy of the Order, may refer to the works of Vesque. Among the Quiineae (which Vesque does not class with the Guttiferae), I have investigated *Touroulia pteridophylla*, Radlk.

Platonia, Pentadesma, Garcinia, Rheedia, Kayea, Mesua, Poeciloneuron, Mammea, and *Touroulia*) ; the occurrence of an inner thickening-lamella (in certain species of *Calophyllum*, in some cases on all sides of the cells, e.g. in *C. Thwaitesii*, Tr. et Pl., in other cases on the outer wall only, e.g. in *C. bracteatum*, Thw.). Formation of papillae on the lower epidermis occurs in *Garcinia Livingstoni*, T. Anders., and *G. polyantha*, Oliv. ; in *Mesua ferrea*, Choisy, there is only an indication of it. A **hypoderm** (one- to many-layered) on the upper side of the leaf is very widely distributed. Vesque met with it in all the species of *Clusia, Cochlanthera, Rengifa, Havetia, Oedematopus, Pilosperma, Montrouziera*, and *Platonia*, as well as in certain species of *Chrysochlamys, Tovomita, Garcinia*, and *Calophyllum*. Regarding the species of *Chrysochlamys*, &c., which possess hypoderm, and the details of the differentiation of the latter, Vesque should be referred to. With respect to the latter point it is only necessary to mention here that the hypoderm of *Oedematopus obovatus*, Tr. et Pl. (Fig. 27, *B*) is formed by a many-layered, spongy, partly green tissue, while that of

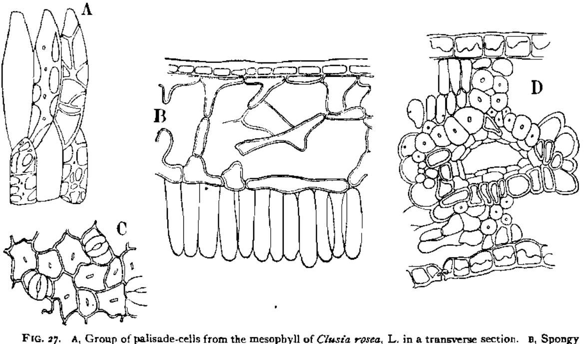

FIG. 27. A, Group of palisade-cells from the mesophyll of *Clusia rosea*, L. in a transverse section. B, Spongy hypoderm from the leaf of *Oedematopus obovatus*, Tr. et Pl. C, Crystal-containing epidermis of the leaf of *Garcinia punctata*, Oliv. D, Transverse section through the leaf of *Calophyllum buxifolium*, Vesque, with a resin-canal accompanied by tracheides and sclerenchymatous fibres.—A, original, the remainder after Vesque.

Clusia insignis, Mart., consists of two layers of rod-shaped sclerenchymatous cells elongated in the direction of the veins.

The **stomata** are almost always, i.e. only with the exception of some species of *Garcinia*, restricted to the lower surface of the leaf. Their guard-cells (also in *Touroulia*) are accompanied on their longitudinal sides by one or several subsidiary cells parallel to the pore. In certain species of *Garcinia* (*G. angolensis*, Vesque, *G. Baikieana*, Vesque, *G. Livingstoni*, T. Anders., *G. ovalifolia*, Oliv., *G. polyantha*, Oliv.) the subsidiary cells are characterized by papillose protuberances, and in some species of *Chrysochlamys* and *Symphonia* by strong striation in the transverse direction relatively to the pore. Besides these features, the following have been made use of by Vesque for specific diagnosis : the varied form of the pair of guard-cells ; the size of the subsidiary cells ; the position of the guard-cells with regard to the subsidiary cells, viz. whether the former are at the same level as the subsidiary cells or are covered by the latter.

Cork-warts have been observed (E. Bachmann) in *Clusia flava* and *Xanthochymus pictorius*.

The vascular bundles of the smaller **veins** are in almost all cases (excepting some few species of *Garcinia*) accompanied by bundles of sclerenchyma or surrounded by a ring of sclerenchyma. It is noteworthy that in *Touroulia pteridophylla*, Radlk. the sclerenchymatous elements detach themselves singly or in bundles from the veins and then run free in the mesophyll. In the majority of the genera of the Order (*Clusia, Cochlanthera, Rengifa, Havetia, Oedematopus, Pilosperma, Balboa, Clusiella, Astrotheca, Chrysochlamys, Tovomitopsis, Tovomita, Symphonia. Montrouziera, Moronobea, Platonia, Allanblackia, Garcinia, Rheedia, Touroulia*) the vascular bundles of the smaller veins are embedded. On the other hand, the genera *Calophyllum, Kayea, Mesua, Poeciloneuron*, and *Mammea* (which are very closely related to one another) have the smaller veins vertically transcurrent; in these a plate of sclerenchyma accompanies the vascular bundle on the upper and lower side, and extends as far as the epidermis. The smaller veins of *Pentadesma* and *Ochrocarpus* should be described as

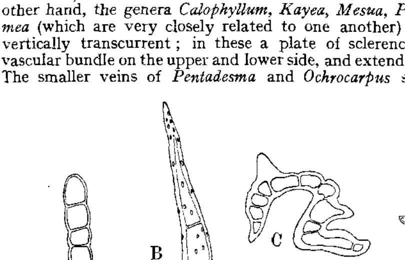

FIG. 28. Hairy covering of the Guttiferae: A, *Calophyllum retusum*, Wall.; B, *C. bracteatum*, Thw.; C, *C. Pseudotacamahaca*, Tr. et Pl.; D, *C. Calaba*, Jacq. (buds); E, *C. tomentosum*, Wight.—After Vesque.

'almost vertically transcurrent by means of sclerenchyma.' In addition to this it should be noted, that in *Ochrocarpus longifolius*, Benth. et Hook, the girder-sclerenchyma spreads out to the right and left below the upper epidermis, and in this manner forms a continuous hypoderm consisting of sclerenchyma-fibres. Enlarged terminal tracheides have been observed in species of *Kayea, Mesua*, and *Rheedia*.

In the majority of cases **oxalate of lime** is present in the mesophyll in the form of clustered crystals. In some genera it is wanting. In others one finds solitary crystals in addition to the clustered crystals, especially round the vascular bundles (*Garcinia, Rheedia, Ochrocarpus, Calophyllum, Kayea*), or solitary crystals exclusively (*Pentadesma, Mesua, Poeciloneuron, Mammea*). A further form of oxalate of lime is represented by small crystals, mostly of prismatic shape, which are contained in the epidermis of the leaf in many species of *Garcinia* (*G. Benthami*, Pierre, *G. cornea*, L., *G. echinocarpa*, Thw., *G. elliptica*, Hook. f., *G. Mannii*, Oliv., *G. punctata*, Oliv., Fig. 27, C, *G. Rumphii*, Pierre, *G. Schefferi*, Pierre, *G. venulosa*, Choisy) and in *Tovomita martinicensis*, Vesque. Lastly, it may be pointed out, that in some species

of *Garcinia* (*G. densiflora*, Vieill., *G. fascicularis*, Wall., *G. Harmandi*, Pierre, *G. Mungotia*, Depl.) clustered crystals are also met with in the epidermis of the leaf.

A **hairy covering** (Fig. 28) is rare in the Order, and consists of clothing hairs only. Glandular hairs are wanting. In *Garcinia Vilersiana*, Pierre and *Touroulia pteridophylla*, Radlk., the clothing hairs are unicellular and short. In *Calophyllum* they are uniseriate, sometimes biseriate at the base, short or long, and often of very curious form. Firstly, simple hairs occur in this genus. But very frequently single cells at the base, the middle, or the end of these simple trichomes are arched out in a papillose manner, and thus a series of forms of hairs arises, ending in the copiously branched hairs of *C. tomentosum*, Wight, and the dichotomously divided hairs of *C. bracteatum*, Thw., *C. Hasskarlii*, Teysm. et Binn., &c.

The occurrence of **secretory canals** or **secretory cavities** or of both together is very characteristic of the leaves of the Guttiferae, with the exception of the Quiineae. These secretory elements are not uncommonly visible even with a lens or the naked eye as transparent lines, small striae or dots. In some members of the Order the secretory canals are restricted to the veins; in others they also run free in the mesophyll, independently of the bundles of the veins. The secretory cavities lie in the meshes of the veins and are met with in the genera *Garcinia* pro parte, *Kayea*, *Mammea*, *Mesua*, *Ochrocarpus* pro parte, *Pentadesma* and *Poeciloneuron*.

The following statements may be made on the form and distribution of the secretory organs in question in the different tribes.

In the genera of the Clusieae (*Clusia*, *Cochlanthera*, *Rengifa*, *Renggeria*, *Havetia*, *Oedematopus*, *Pilosperma*, *Balboa*, *Clusiella*, *Astrotheca*, *Chrysochlamys*, *Tovomitopsis*, *Tovomita*) the secretory canals, as a rule, run free in the mesophyll, independent of the veins, frequently meeting the latter at an acute angle and sometimes anastomosing with one another; the resin-canals are sometimes also found in the hypoderm and still more rarely (*Clusia eugenioides*, Pl. et Lind., *C. flava*, L., *C. minor*, L., *C. Pana-Panare*, Choisy; *Havetia laurifolia*, H. B. K.; *Tovomita guianensis*, Aubl., *T. Spruceana*, Tr. et Pl.; all according to Vesque) in the parenchyma of the veins. It is still unknown how the genus *Oxystemon*, which is classed with the Clusieae, behaves in this respect; the 'folia obsolete pellucido-punctata' rather lead one to infer the occurrence of secretory cavities.

Of the genera of the Moronobeae *Platonia* agrees with the Clusieae, in that the secretory canals in this genus have an entirely free course in the mesophyll. *Pentadesma*, belonging to the same tribe, has secretory cavities only and no secretory canals in the leaf. The four remaining genera of the tribe (*Symphonia*, *Montrouziera*, *Moronobea*, and *Allanblackia*) are characterized by the fact that the secretory canals are placed above the vascular system in the veins. Moreover, in certain species of *Symphonia* and *Montrouziera*, according to Vesque, smaller secretory canals occur in the mesophyll; it still remains an open question whether these latter are not merely accidental branches of the secretory canals which accompany the vascular bundle-system, such as Blenk has observed in *Moronobea* and *Symphonia*.

The following facts may be cited regarding the three genera of the Garcinieae:

(1) In the very numerous species of the genus *Garcinia*, Vesque almost always met with secretory canals running free in the mesophyll; *G. travansorica*, Bedd. is the sole exception in which the balsam-canals run in the veins alone. In a relatively large number of species of *Garcinia* secretory canals also occur in the veins, besides those running free in the mesophyll. Lastly, a series of species of *Garcinia* possess secretory cavities in addition to the secretory canals, viz. *G. Beccarii*, Pierre, *G. Griffithii*, Th. Anders., *G. Hanburyi*, Hook. f., *G. lateriflora*, Bl., *G. Loureiri*, Pierre, *G. malaccensis*, Hook. f., *G. Mannii*, Oliv., *G. Oliveri*, Pierre, *G. paniculata*, Roxb., *G. parvifolia*, Miq., *G. punctata*, Oliv., *G. Schomburgkiana*, Pierre, *G. succifolia*, Kurz, and *G. Trianii*, Pierre, according to Vesque, as well as *G. anomala*, Tr. et Pl. and *G. elliptica*, Wall., according to Blenk.

(2) In the species of the genus *Rheedia*, the secretory canals run free in the mesophyll, sometimes in the parenchyma of the veins as well.

(3) In the genus *Ochrocarpus*, Vesque states that secretory cavities occur either alone (*O. africanus*, Oliv., and *O. longifolius*, Benth. et Hook.), or together with secretory canals in the veins (*O. eugenioides*, Vesque), or ' glandulae canaliformes in areolis venarum,' i.e. secretory canals in the mesophyll (*O. excelsus*, Vesque).

Lastly, the fourth tribe, that of the Calophylleae, falls into two sharply divided groups according to the secretory organs. The first of these consists of the genera *Kayea*, *Mesua*, *Mammea*, and *Poeciloneuron*. In these genera, secretory cavities are always found in the meshes of the network formed by the veins. In certain species of *Kayea*, *Mesua*, and *Mammea*, secretory canals occur in addition in the parenchyma of the veins, occasionally that of the principal veins only, and in one species (*Kayea macrantha*, Baill.) secretory canals are also found running free in the mesophyll. In the fifth genus, *Calophyllum*, secretory cavities are absent. In place of them, in all species of this genus, one finds secretory canals running free in the mesophyll between the lateral veins, and in some species the canals are also present in the veins. The secretory canals which run in the mesophyll of *Calophyllum* are always accompanied by broad spiral tracheides, with which sclerenchyma-fibres are frequently associated (Fig. 27, *D*).

3. STRUCTURE OF THE AXIS. The following facts are known regarding the structure of the **wood**, and are based on the investigation of species of the genera *Garcinia* (including *Hebradendron*), *Symphonia* (including *Chrysopia*), *Calophyllum*, *Mesua*, *Mammea*, and *Touroulia* (*T. pteridophylla*, Radlk.). A transverse section of the xylem-mass shows (*a*) vessels, which are isolated or arranged in radial rows and have lumina of different sizes (maximum diameter = ·036 mm. in *Garcinia merguensis*, Wight, ·012 mm. in *Mammea americana*, L.); (*b*) 1–4-seriate medullary rays, and (*c*) usually also (exception, *Touroulia*) tangential bands of wood-parenchyma. The perforations of the vessels are simple (even in *Quiina*, according to Engler). The vessel-wall, where it is in contact with parenchyma of the medullary rays, bears bordered pits (*Garcinia*, *Symphonia*, *Touroulia*) or large simple pits (*Calophyllum*, *Mesua*). The pitting of the wood-prosenchyma is difficult to recognize, on account of the narrow lumeu of the cells. In *Calophyllum*, *Mesua*, *Garcinia*, and *Touroulia* the pits of the prosenchyma have narrow borders, in *Symphonia* they are simple. Chambered crystal-parenchyma has been observed in the wood of *Symphonia globulifera*, L., and *Mesua speciosa*, Choisy.

Regarding the structure of the **cortex**, statements are found in the works of Möller, Douliot, and K. Müller. The cork arises either in the epidermis (species of *Havetiopsis*, *Platonia*, and *Calophyllum*) or subepidermally in the outermost cell-layer of the primary cortex (species of *Mesua*, *Oedematopus*, *Pilosperma*, *Tovomita*, *Quiina*). In *Tovomita*, *Pilosperma*, *Oedematopus*, and *Quiina* the cork consists of few layers, of which the second exhibits unusually strongly thickened outer, tangential walls, but in *Mesua* the cork consists of cells with wide lumina and thin walls. Phelloderm, consisting of cells sclerosed in the form of a U, has been observed in *Calophyllum*. Sclerenchyma is usually abundantly developed in the cortex. If I understand K. Müller rightly, a composite and continuous ring of sclerenchyma is present in the pericycle, in the species of *Clusia* investigated by him, in *Tovomita umbellata*, Benth., in a few species of *Garcinia* and in *Mesua ferrea*, L., likewise, according to Möller, in *Calophyllum Inophyllum*, L., but not in all the members of the Order. The secondary bast sometimes (*Calophyllum Inophyllum*) contains plates of sclerenchyma consisting of groups of bast-fibres and stone-cells. As in the leaf, oxalate of lime is found in the cortex in the form of clustered and solitary crystals.

In the Guttiferae (excluding the Quiineae) the **secretory organs of the axis** [1], like those of the leaf, consist of resin-canals and of resin-cavities. The

[1] According to Van Tieghem's work, which corrects the statements of K. Müller and the earlier authors.

latter have hitherto only been observed in the primary cortex of *Mammea*, but may perhaps occur also in the same position in the other genera, which possess secretory cavities in the leaf. Secretory canals have been met with in the pith and in the primary cortex in all the Guttiferae hitherto investigated with regard to their stem-structure; only in *Pilospermum caudatum* was Van Tieghem unable to find any medullary secretory canals. Besides the medullary and cortical secretory canals, resin-canals also occur in the bast in certain genera, and in that case either only in the secondary bast or in both primary and secondary bast.

The following have no secretory canals in the bast: *Clusia* (including *Arrudea*), *Tovomita*, *Havetiopsis*, *Pilosperma*, *Pentadesma*, *Oedematopus*, also *Allanblackia*, according to K. Müller. Secretory canals are present in the secondary bast in *Mesua*, *Havetia*, *Garcinia* (including *Xanthochymus*), *Rheedia*, *Calophyllum*, *Symphonia*. The primary and secondary bast contains secretory canals in *Mammea* and *Ochrocarpus*.

In order to avoid erroneous statements, it may be remarked here, that Van Tieghem observed the formation of tyloses in the cortical secretory canals of *Mammea americana* and other members of the Order, so that the canals are obliterated and become indistinguishable. The stopping up of the secretory canals is brought about here, as in other Orders (Anacardiaceae, Dipterocarpeae), by some of the epithelial cells growing out into papillae, which, penetrating into the oil-canal, finally come into contact with one another and completely fill up the canal.

In connexion with the secretory canals of the axis, the resin-canals in the root may be briefly mentioned. In regard to the latter Van Tieghem makes the following statements: secretory canals exclusively in the primary cortex in *Clusia*; secretory canals in the primary and secondary bast, as well as a secretion in the subepidermal and the innermost cell-layer of the primary cortex in *Garcinia*, *Xanthochymus*, and *Rheedia*; secretory canals in the primary cortex and in the primary and secondary bast in *Mammea*, *Calophyllum*, and *Ochrocarpus*.

The genus *Quiina* (including *Touroulia*) has no resin-canals; in their place intercellular spaces filled with mucilage, as Trécul had already observed, occur in the branches of certain species (*Q. obovata* and *Q. Decaisneana*, and in *Touroulia pteridophylla*); they are found at the centre and often also at the periphery of the pith in the axis and in the pith, or in the parenchyma situated above the vascular system of the petiole and of the larger veins; these intercellular spaces, according to Engler and my own observation, are differentiated as canals in *Touroulia*. The genus *Sphaerosepalum*, which was classed by Baker with the Guttiferae but was transferred by Warburg to the Bixaceae, also contains medullary mucilage-canals but no resin-canals.

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TERNSTROEMIACEAE.

1. Review of the Anatomical Features. The Ternstroemiaceae have no special anatomical characters common to all of them. As regards the structure of the leaf and axis in general the following features should be pointed out.

In the Bonnetieae the stoma is accompanied by two subsidiary cells which are parallel to the pore, in other cases it is surrounded by three or four epidermal cells which are differentiated like subsidiary cells, and in others again it is surrounded by ordinary epidermal cells in varying number. The vascular bundles of the smaller veins are either embedded in the mesophyll (*Camellia, Caryocar, Gordonia, Marcgravia, Ternstroemia*), or vertically transcurrent (*Caraipa, Kielmeyera, Saurauja*). Sclerenchymatous cells of varied shape (Fig. 29, *B–D*), e.g. branched sclerenchyma-cells, sclerenchyma-fibres, &c., are very widely distributed in the mesophyll (in species of *Anneslea, Camellia, Cleyera, Freziera, Gordonia, Laplacea, Marcgravia, Norantea, Pelliciera, Schima, Souroubea, Ternstroemia*, and *Visnea*). It may be mentioned in passing that these elements occur also in the parenchyma of the pith and cortex. In the tissues of the axis mentioned they are sometimes replaced by ordinary stone-cells; the latter occasionally form horizontal diaphragms in the pith. In connexion with the above characters, which are important for the diagnosis of the Order, mention should also be made of the following, which may be employed for specific diagnosis: the occurrence in the leaf of hypoderm, of papillose differentiation of the epidermis, of a mucilaginous epidermis, and of arm-palisade-parenchyma (Fig. 29, *A*).

In the Marcgravieae and Sauraujeae (excl. *Stachyurus*) as well as in *Pelliciera*, oxalate of lime is present in the form of raphides, which in *Pelliciera* and *Saurauja* are in part replaced by styloids. In the remaining tribes ordinary solitary and clustered crystals occur.

The hairy covering consists of simple unicellular hairs (*Gordonia, Camellia*), of multicellular, branched trichomes (*Saurauja*), of small unicellular structures resembling stellate hairs or small scales (*Caraipa, Marila*), of small scale-like trichomes, which belong to the category of tufted hairs (*Saurauja*), and of multiseriate shaggy hairs (*Saurauja*). Glandular hairs have not been observed in the Order. On the other hand, the leaf-teeth are occasionally differentiated as glands, and in the Marcgravieae large nectaries visible even to the naked eye are found on the lower side of the leaf. The cork-warts must not be confounded with the latter; they have been observed on the lower side of the leaf in many members of the Order (species of *Anneslea, Camellia, Caryocar, Eurya, Marcgravia*, and *Ternstroemia*).

Internal secretory organs occur in four forms in the Order; firstly, as cells with mucilaginous membrane, which occur in many species in the epidermis, or in the hypoderm of the leaf, in some cases (*Archytaea* and *Bonnetia*) in the mesophyll also; secondly, as secretory cells (in the midrib of the leaf of species of *Marcgravia*); thirdly, as schizogenous secretory cavities in the leaf-tissue; and fourthly, as schizogenous resin-canals in the branch and in the larger veins of the leaf (both kinds in the genera [of the Bonnetieae] *Kielmeyera, Caraipa, Mahurea, Marila*, and *Haploclathra*). Transparent dots in the leaf are caused by the schizogenous secretory cavities, and sometimes likewise by the mucilaginous epidermal cells and by the sclerenchyma-cells of the mesophyll.

Regarding the structure of the wood special mention should be made of the fact that most members of the Order possess scalariform perforations with numerous bars in their vessels; simple perforations, however, also occur in certain genera, either in a subordinate degree or as the prevalent form, or they are present to the exclusion of the other type. The nature of the vessel-wall, where it is in contact with parenchyma, varies, either ordinary bordered

pits being present at these places (*Marcgravia, Norantia, Saurauja, Stachyurus, Ternstroemia* and *Visnea*), or large simple pits with transitions to bordered pits (*Caryocar, Gordonia, Kielmeyera, Stuartia*); other features showing similar variation are: the pitting of the wood-prosenchyma, which is either simple (*Caryocar*) or more or less distinctly bordered; the development of wood-parenchyma and the breadth of the medullary rays; and lastly, the place of origin of the cork, the phellogen being formed either by the epidermis, or by the sub-epidermal cell-layer of the cortex, or by a layer of cells situated in the middle of the primary cortex, or lastly by the (pericyclic) cell-layer immediately on the inner side of the primary hard bast. In the pericycle, isolated groups of bast-fibres, a ring of bast-fibres or a composite and continuous sclerenchymatous ring may occur.

2. STRUCTURE OF THE LEAF. No connected research on the leaf-structure of this Order exists. The following description is based on my own investigation of the detailed structure of the leaf in some few representatives of the six tribes of the Order (*Caryocar glabrum*, Pers.; *Marcgravia picta*, Willd.; *Ternstroemia dentata*, Sw.; *Saurauja napaulensis*, DC.; *Pelliciera* sp., Sutton Hayes n. 76, Panama; *Gordonia excelsa*, Bl.; *Kielmeyera angustifolia*, Pohl), further, on some of my own casual observations on certain anatomical features in species other than those just named, as well as on the statements of Juel as to some Marcgravieae, of Vesque regarding the species of *Eurya*, and of Blenk as to special features in the leaf of the Ternstroemiaceae.

The **mesophyll** is as a rule bifacial in structure. In *Caryocar glabrum* and in *Pelliciera* sp., there is a tendency to centric leaf-structure. In *Kielmeyera angustifolia* the whole mesophyll is formed by palisade-tissue. In leaves of bifacial structure the palisade-tissue consists of one layer, and in that case either of long, e.g. in *Gordonia excelsa*, or short cells, e.g. in *Marcgravia picta*, or of more than one layer with short cells, e.g. in *Saurauja napaulensis*. The palisade-tissue of *Saurauja napaulensis* (Fig. 29, *A*) contains the arm-palisade-cells of Haberlandt in a well-marked form. The folds (of the wall) projecting into the cell-lumen here appear like portions of simple longitudinal walls of the palisade-cells and only indicate that they are of the nature of folds by a small swelling at their ends; on superficial observation one appears to be dealing with ordinary short palisade-cells, with their longitudinal walls provided in some cases with circular perforations. The occurrence in the mesophyll of sclerenchyma-cells (Fig. 29, *B–D*), which in some cases are branched, is of very wide distribution. Among the plants investigated by me these elements occur in the above-named species of *Gordonia, Marcgravia, Pelliciera* and *Ternstroemia*. Blenk met with them in certain species of *Anneslea, Cleyera, Freziera, Gordonia, Laplacea, Marcgravia, Norantea, Pelliciera, Schima, Souroubea, Ternstroemia* and *Visnea*, and Vesque found them in some species of *Eurya*. In form the sclerenchymatous elements in question are either stellately branched on all sides, and in that case are more or less similar to the so-called internal hairs of the Nymphaeaceae; or they resemble rod-cells or fibres and then mostly extend perpendicularly to the leaf-surface through the palisade-tissue or even through the whole thickness of the leaf and frequently give rise to transparent dots; or, on the other hand, e.g. in *Souroubea guianensis*, Aubl., they are fibre-like and traverse the mesophyll in all directions and quite irregularly. In *Pelliciera* sp. very peculiar sclerenchyma is found in the mesophyll. In two planes which are parallel to the surface of the leaf and situated below the first layer of the mesophyll on both sides, numerous long, straight sclerenchyma-cells occur, which are pointed at the ends, unbranched, and hence resemble bast-fibres. These elements are arranged parallel to one another and at the same time in an oblique direction with regard to the median vein.

Blenk states that spicular cells occur in the following members of the Order: *Cleyera grandiflora*, Hook. f. et Th., *C. ochnacea*, DC.; *Freziera undulata*, Sw.; *Gordonia acuminata*, Choisy, *G. excelsa*, Bl., *G. Haematoxylon*, Sw. (=*Laplacea Haematoxylon*, G. Don), *G. obtusa*, Wall., *G. Wallichii*, DC.; *Schima Noronhae*, Reinw. These spicular cells traverse the palisade-tissue or often even the whole thickness of the leaf perpendicularly to its surface; according to my own investigations they are either like rod-cells and scarcely branched (*Freziera undulata*, Sw., Fig. 29, *B*),

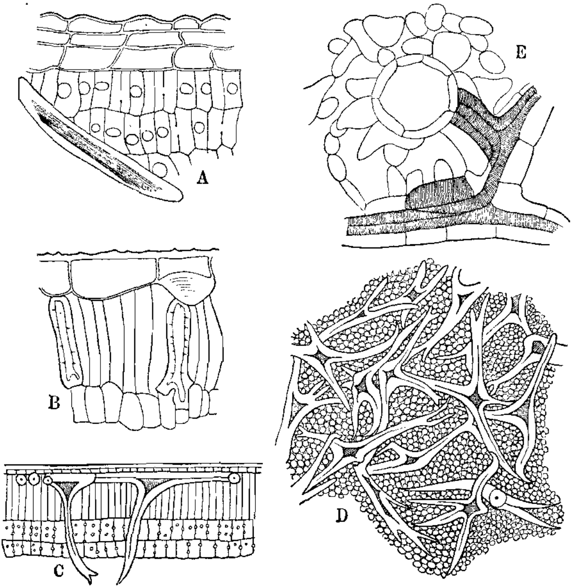

FIG. 29. A, Transverse section through part of the leaf (upper side) of *Saurauja napaulensis*, DC, with arm-palisade-parenchyma. B, Part of a transverse section of the leaf of *Freziera undulata*, Sw., with a mucilaginous epidermal cell and with rod-shaped spicular cells. C–D, Spicular cells of *Cleyera grandiflora*, Hook. fil. et Thoms.; C, in a transverse section of the leaf; D, in a superficial section of the upper side of the leaf. E, Secretory cavity in a mesh between the veins of *Caraipa fasciculata*, Camb.: tracheae extend from the vascular bundles of the veins to the secretory cavity.—Original.

or they are more branched (*Cleyera grandiflora*, Hook. fil. et Th., Fig. 29, *C–D*); in the latter case, the branches are spread out in a plane traversing the palisade-tissue at right-angles and lying parallel to the leaf-surface immediately below the epidermis of the upper side. Branched sclerenchyma-cells, in part analogous to the hairs of the Nymphaeaceae, are mentioned by Blenk in the following species: *Anneslea crassipes*, Choisy; *Marcgravia parviflora*, Rich. var., *M. picta*, Willd. (in these they are only slightly branched and only found in the midrib); *Norantea adamantium*, Camb., *N. brasiliensis*, Choisy, *N. guianensis*, Aubl., *N. japurensis*,

Mart. (in these they are likewise little branched and are only in the midrib); *Ternstroemia japonica*, Thunb., *T. japonica*, Sieb. et Zucc., *T. Lushia*, Buch.-Hamilt. In *Visnea Mocanera*, L. f., Blenk merely refers to sclerenchyma-cells. The groups of cells in the leaf-tissue of *Pelliciera* sp. (Sutton Hayes), described by Blenk as roundish nests of sclerenchyma, are spherical groups of enlarged terminal tracheides with bordered pits. The sclerenchyma-cells observed by me in the leaf-tissue of the above-named species of *Gordonia*, *Marcgravia*, and *Ternstroemia*, belong to the category of branched sclerenchyma-cells; as do also the sclerenchymatous elements in the mesophyll of *Camellia Thea*, Link, which, as is well known, form an important, though not absolutely constant, character of the genuine tea-leaf. The sclerenchyma which Vesque met with in the leaves of *Eurya phyllanthoides*, Bl. and *E. clandestina*, Bl. consists of fairly isodiametric or very shortly branched cells. The special sclerenchyma-fibres in the leaf of *Souroubea guianensis* and *Pelliciera* sp. have already been fully discussed above.

The **epidermal cells** of the leaves have either straight or undulated lateral walls. Papillose differentiation of the epidermal cells has been observed in *Saurauja napaulensis* on the upper side of the leaf, in *Haploclathra leiantha*, Benth. on the lower side. According to Vesque hypoderm is present on the upper side of the leaf in *Eurya castaneifolia*, Vesque, *E. cavinervis*, Vesque, *E. sanguinea*, Vesque, *E. sandvichensis*, A. Gray, and *E. symplocina*, Bl.; according to my own observations hypoderm is present in *Archytaea triflora*, Mart. (on the upper side and two-layered), in *Bonnetia anceps*, Mart. et Zucc. (on the upper side and one-layered), in *Pelliciera* sp. (on both sides and one-layered) and in *Saurauja napaulensis* (on the upper side and two-layered).

Gelatinization of the epidermal cells of the leaf is by no means rare in the Order. It is described by Blenk in several species of *Norantea* (*N. adamantium*, Camb., *N. brasiliensis*, Choisy, *N. guianensis*, Aubl., and *N. japurensis*, Mart.), by Vesque for those species of *Eurya* which possess no hypoderm, and it occurs also in *Gordonia excelsa*, *Caryocar glabrum*, and *Freziera undulata*. In *Archytaea triflora* individual cells and in *Bonnetia anceps* all the cells of the hypoderm have mucilaginous inner walls. It may be added that cells with mucilaginous membrane also occur in the mesophyll of certain species. In *Archytaea triflora*, mucilaginous cells are found in the mesophyll which is formed entirely by palisade-tissue; mucilaginous cells occur also in the spongy parenchyma of the bifacially constructed leaf of *Bonnetia anceps*.

Stomata are usually present only on the lower surface of the leaf. They have been observed in small numbers on the upper side of the leaf of *Marcgravia picta*. The type of stoma is not uniform. While in the Bonnetieae, the Rubiaceous type is quite generally[1] distributed (i.e. the pair of guard-cells is accompanied by subsidiary cells, which lie parallel to the pore), in the members of the remaining tribes the stoma is surrounded by from three to six epidermal cells, which in certain species (but not in all) are differentiated like subsidiary cells. Thus the guard-cells of *Gordonia excelsa* have three distinct subsidiary cells; the stomatal apparatus of *Marcgravia picta* is surrounded by four epidermal cells differentiated like subsidiary cells; in *Saurauja napaulensis*, also, the stomata are surrounded by three subsidiary cells, rarely by a larger number of epidermal cells; in *Caryocar glabrum*, on the other hand, one meets with three or four, in *Ternstroemia dentata* and in the leaf of the tea-plant with four to six not specially conspicuous epidermal cells surrounding the guard-cells.

The vascular bundles of the **veins** are, as a rule, accompanied by varying amounts of sclerenchyma with thick walls or wide lumina, and are either embedded in the mesophyll (in *Caryocar*, *Gordonia*, *Marcgravia* and *Ternstroemia*,

[1] The following Bonnetieae were investigated by me with regard to the occurrence of the Rubiaceous type: *Bonnetia anceps*, Mart. et Zucc., *Archytaea triflora*, Mart., *Kielmeyera angustifolia*, Pohl, *K. paniculata*, Rusby, *Caraipa fasciculata*, Camb., *Mahurea palustris*, Aubl., *Marila racemosa*, Sw., and *Haploclathra leiantha*, Benth.; thus species of all seven genera are included.

and also *Camellia Thea*), or are vertically transcurrent (in *Kielmeyera* and *Saurauja*, and also in *Caraipa fasciculata*, Camb.). Enlarged terminal tracheides have been observed not uncommonly, e.g. in *Pelliciera* sp.

The general features of the leaf-structure having been discussed we may now refer to the interesting fact, demonstrated by Juel, that the dimorphic leaves of *Marcgravia* show different types of anatomical structure. The large leaves of the fertile branches of *Marcgravia coriacea*, Vahl have a one-layered hypoderm on both sides of the leaf; the chlorophyll-bodies in the assimilatory tissue are only 5–9 μ in diameter. In the same species, on the other hand, the small leaves belonging to the root-producing and climbing sterile branches have no hypoderm, while the epidermal cells of the upper side of the leaf are papillose and accompanied by stomata; further, the chlorophyll-grains in the small leaves are 20 μ long and 10 μ broad.

Oxalate of lime is excreted in the form of raphides, styloids, clustered crystals, and ordinary solitary crystals. Raphide-sacs are stated by Blenk to occur in almost all the representatives of the two tribes Marcgravieae (in *Marcgravia, Souroubea, Norantea*) and Saurau jeae examined by him (in *Actinidia* and *Saurauja*; but not in *Stachyurus praecox*, Sieb. et Zucc., where raphides are absent in axis and leaf) as well as in the genus *Pelliciera* belonging to the tribe Gordonieae. These raphide-sacs are mostly characterized by mucilaginous contents and frequently give rise to pellucid dots in the leaf. It is worthy of note, that in certain species of *Saurauja* and likewise in *Pelliciera* sp., the raphide-cells are partly replaced by elongated cells, lying parallel to the surface of the leaf and containing either a single acicular crystal (styloid) or even—in species of *Saurauja* according to Blenk—a series of apparently cubic crystals lying in a row. The features presented by the crystals in the genera of the remaining tribes are briefly as follows. In *Caryocar glabrum*, belonging to the tribe Rhizoboleae, I have only met with ordinary solitary crystals in the mesophyll and accompanying the vascular bundles of the veins. In *Ternstroemia dentata* I found clustered crystals only; Blenk found the same in *Visnea Mocanera*, L., belonging to the same tribe (Ternstroemieae). Among the Gordonieae Blenk describes clustered crystals in *Stuartia monadelpha*, Sieb. et Zucc., solitary crystals in other species of the same genus; I have only observed clustered crystals in *Gordonia excelsa* and *Camellia Thea*. *Kielmeyera angustifolia*, of the tribe Bonnetieae, contains clustered crystals in the leaf-tissue. Mention should also be made of the fine acicular crystals, which occur in the epidermis of the dried leaf of *Anneslea crassipes*, Choisy, and are mostly grouped in bundles; nothing further is known as to their nature, but they dissolve neither in *eau de Javelle* nor in sulphuric acid; Vesque met with sphaerocrystalline masses, which likewise require further investigation, in the mucilage of the epidermal cells in numerous species of *Eurya* (e.g. in *Eurya acuminata*, DC. var. *Wallichiana*).

Internal **secretory organs** appear under four forms in this Order, as mucilaginous cells, secretory cells, schizogenous resin-cavities, and schizogenous resin-canals. The cells with mucilaginous membrane, which occur not only in the epidermis and hypoderm, but also in the middle of the mesophyll, have already been discussed above. Blenk has observed secretory cells in the neighbourhood of the midrib of the leaf in species of *Marcgravia* (*M. picta*, Willd. and *M. parviflora* Rich. var.). These elements have a roundish or oval shape; their colourless contents do not dissolve in alcohol, but easily in ether (fat ?). The schizogenous resin-canals and resin-cavities occur only in the Bonnetieae, where they are present in the majority of the genera, namely, in *Kielmeyera, Caraipa, Mahurea, Marila* and *Haploclathra*, but not in *Bonnetia* and *Archytaea*.

The secretory canals in the branches have been investigated by Van Tieghem: they will be discussed in detail in the section on the structure of the axis. According

to my own investigations, which extended to the species of the seven genera of the Bonnetieae already named in the note on p. 130, the secretory canals pass out from the stem into the leaf, where they are occasionally to be met with above or below the vascular bundle-system, even in the small veins; but they are never found running free in the mesophyll, as is the case in many Guttiferae. But in their place (and I publish the fact here for the first time) schizogenous secretory cavities of spherical or elongated form occur in the mesophyll of those Bonnetieae which are provided with resin-canals. These schizogenous secretory cavities are usually visible even to the naked eye, as transparent dots or lines, in one group of the species without further preparation, in another group after cutting the leaf, while in a third group of species they can only be demonstrated by microscopic examination. I have determined the presence of these secretory cavities in the following species: *Kielmeyera angustifolia*, Pohl (folia epunctata) and *K. paniculata*, Rusby (f. pellucido-punctata et lineolata); *Caraipa fasciculata*, Camb., and *C. glabrata*, Mart. (f. epunctata); *Mahurea palustris*, Aubl. (f. obtecte pellucido-punctata et lineolata); *Marila racemosa*, Sw. (f. pellucido-punctata et lineolata), *M. laxiflora*, Rusby (f. pell.-punct.); *Haploclathra leiantha*, Benth. (f. pell.-punct.), *H. paniculata*, Benth. (f. obtecte pell.-punct.). The spherical secretory cavities of the two species of *Caraipa* cited (Fig. 29, *E*) are specially noteworthy in that they occur singly in each mesh of the veins, and are surrounded by loose, spongy tissue, and in that spiral tracheides adjoin the secretory cavity on one or on several sides, these tracheides branching off from the vascular bundles of the veins which bound the mesh; a similar arrangement also occurs, as is well known, in the Guttiferous genus, *Calophyllum*. Lastly, attention may be drawn to the fact that the genera of the Bonnetieae, apart from *Bonnetia* and *Archytaea*, approximate closely to the Guttiferae in their anatomy by the possession of resin-canals and secretory cavities; moreover, the same type of stoma is found in both these orders, namely the Rubiaceous type. Whether this circumstance is of importance for the further elaboration of the Natural System, can only be determined by a comparison with the exomorphic features. At any rate, those Bonnetieae which are distinguished by the possession of schizogenous resin-receptacles, are also connected, with the other Bonnetieae, i. e. the two genera *Bonnetia* and *Archytaea*, by means of a further anatomical feature, the type of stoma.

Although a **hairy covering** is not exactly common in this Order, yet various forms of hairs have been shown to occur. In *Caryocar glabrum* the formation of hairs is only indicated by single cells of the lower epidermis exhibiting a small papillose apiculus. *Gordonia excelsa* and the leaf of the tea-plant possess long unicellular thick-walled hairs. Variously branched trichomes, which have thin walls and wide lumina and consist of relatively short cells, occur in *Saurauja napaulensis* (Fig. 30, *A*). Specially characteristic hairs have been observed in *Marila racemosa*, *Caraipa fasciculata*, and *C. glabrata* (Fig. 30, *B*), namely, trichome-structures resembling small stellate hairs or scales, and usually consisting of only one cell besides a short stalk-cell, which is sometimes (but not always) present; this cell is produced into fairly numerous arms, some of these being forked, and all of them lying in one plane; in *Caraipa glabrata* I have, in isolated cases, also met with a secondary, vertical division-wall in the shield. O. Bachmann has described entirely different hairs in *Saurauja spadicea*, Bl., namely, multicellular, scale-like trichomes, which properly belong to the category of tufted hairs; their ray-cells, which are fairly thin-walled and free at their ends, and which, moreover, now and then show a transverse wall, are spread out horizontally, and, lying one above another in more than one layer, form a small scale-like structure (Fig. 30, *C*). Lastly, we may mention the shaggy hairs of *Saurauja napaulensis* (Fig. 30, *D*), which vary in length, are conical or filiform, and pointed at their ends; the superficial cells, especially at the end of the hair, have projecting, papillose tips.

Glandular hairs have not been observed in the Order. Of the glands, which Wittmack (in 'Flora brasiliensis,' vol. xii, 1, p. 214 et seq.) describes[1] as occurring

[1] Cf. Delpino, Mem. Accad. Bologna, 1886, p. 304.

in varying numbers on the leaves in species of the genera ***Marcgravia, Norantea, Ruyschia,*** and ***Souroubea*** (Marcgravieae), those of ***Marcgravia,*** at any rate, are in part identical with cork-warts (e.g. according to my own investigation, those of *M. Sintenisii*, Urb., in which plant the lower side of the leaf bears abundant black dots owing to the organs in question), the cells of which are filled with brown tanniniferous contents. Similar structures resembling cork-warts or lenticels had previously been observed in other members of the Order by Borzi, E. Bachmann, and others, e.g. in *Anneslea crassipes, Camellia axillaris* and *C. japonica, Caryocar glabrum, Eurya latifolia* and *Ternstroemia dentata.* True nectaries, however, of large size also occur in the Marcgravieae; they are present in various positions on the lower side of the leaf as circular or elliptical depressed spots. I have examined them in detail in *Norantea droseriformis*, Rusby. The depression, which is often filled with a brown secretion, is lined by a small-celled epidermis, which in part contains mucilage; adjoining the epidermis we find numerous sclerosed and pitted parenchymatous cells, the latter being in connexion with the bundles of the veins. In addition to the nectaries mentioned above, the leaf-teeth also figure as

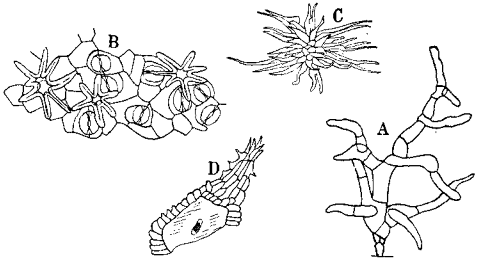

FIG. 30. *Hairy covering of the* Ternstroemiaceae. A, branched trichome of *Saurauja napaulensis*, DC.; B, lower epidermis of the leaf of *Caraipa glabrata*, Mart., with stellate hairs; C, scale of *Saurauja spadicea*, Bl.; D, shaggy hair of *Saurauja napaulensis*, DC.—Original.

secretory organs, e.g. in *Camellia japonica*; they contain the termination of a vascular bundle in connexion with an epithemoid tissue, and above the latter a secretory epidermis of palisade-like, radially elongated cells.

3. Structure of the Axis. Besides my own general preliminary investigations on the structure of the **wood** (in species of *Caryocar, Marcgravia, Norantea, Ternstroemia, Visnea, Saurauja, Stachyurus, Stuartia, Gordonia,* and *Kielmeyera*), there are earlier researches by Molisch on species of *Ternstroemia* and *Camellia* and more recent work, which is unfortunately not very clearly presented, by Hitzemann on species of *Visnea, Ternstroemia, Cleyera, Freziera, Eurya, Actinidia, Saurauja, Stachyurus, Stuartia, Schima, Gordonia, Laplacea,* and *Camellia.* The last-named memoir also contains statements regarding the structure of the cortex.

The vessels have lumina of varied size (maximum diameter = ·09 mm. in *Kielmeyera coriacea*, Mart.; ·03 mm. in *Ternstroemia japonica*, Thunb.). The breadth of the medullary rays also varies. In *Marcgravia* and *Norantea*, in addition to narrow medullary rays, I have observed broad, 5–6-seriate rays, but in the remainder of the species investigated by me, narrow, 1–3-seriate rays only. Broad, 5–7-seriate medullary rays are also stated by Molisch to

occur in *Ternstroemia meridionalis.* The nature of the pitting found on the vessel-wall where it is in contact with the parenchyma of the medullary rays also varies; *Marcgravia, Norantea, Ternstroemia, Visnea, Saurauja,* and *Stachyurus* have bordered pits on these walls, while *Caryocar, Stuartia, Gordonia,* and *Kielmeyera* have large simple pits with transitions to bordered pits. The perforations of the vessels are scalariform in most members of the Order. According to the investigations hitherto carried out scalariform perforations appertain especially to the members of the Ternstroemieae, Saurauj eae, Gordonieae, and Marcgravieae, simple perforations to the Rhizoboleae and Bonnetieae; in almost all the Ternstroemiaceae, however, a tendency to the formation of scalariform perforations appears to be present, for even in the two tribes last named scalariform perforations with few bars are usually present in subordinate numbers side by side with the simple perforations.

Exclusively scalariform perforations, which sometimes have very numerous bars, have been observed in species of *Visnea, Cleyera, Freziera, Ternstroemia,* and *Eurya* (Ternstroemieae); *Actinidia, Saurauja,* and *Stachyurus* (Saurau jeae); *Stuartia, Schima, Gordonia, Laplacea, Camellia* (Gordonieae). Simple perforations have been found in species of *Marcgravia*—exclusively; *Norantea*—together with predominating, scalariform perforations which have as many as nine bars (Marcgravieae); *Caryocar*—together with 1–2-barred perforations in the neighbourhood of the primary wood (Rhizoboleae); *Actinidia*—together with scalariform perforations (Saurau-jeae); *Kielmeyera*—exclusively simple or together with scalariform openings, and *Marila*—exclusively simple (Bonnetieae).

Spiral thickening has been met with on the vessel-wall in *Stachyurus praecox,* Sieb. et Zucc., and *Ternstroemia japonica,* Thunb., on the ends of the segments of the vessels in *Visnea Mocanera,* L., and *Stuartia monadelpha,* Sieb. et Zucc. The wood-parenchyma is usually little developed, but more abundantly in *Stuartia.* Regarding the pitting of the wood-prosenchyma the following statements are derived from my own observations. Typical bordered pits occur in *Ternstroemia Visnea, Saurauja, Actinidia, Stachyurus, Stuartia,* and *Gordonia,* simple pits in *Caryocar.* The pits of the prosenchyma of *Marcgravia, Norantea,* and *Kielmeyera* are small but usually distinctly bordered. Septation of the prosenchyma by means of delicate cross-walls has been observed in *Marcgravia, Norantea,* and *Caryocar.*

The following facts should be mentioned regarding the structure of the **cortex.** The place of origin of the cork varies, but in most of the Ternstroemiaceae (species of *Ruyschia, Visnea, Ternstroemia, Freziera, Eurya, Actinidia, Saurauja, Schima, Gordonia, Bonnetia, Kielmeyera, Caraipa,* and *Marila*) the subepidermal cell-layer becomes the phellogen. In *Haploclathra,* on the other hand, the periderm arises in the middle of the primary cortex, in *Camellia* in the pericycle on the inner side of the primary hard bast. The cork-cells vary in their nature. They are not uncommonly thickened on their inner tangential walls (*Camellia japonica, Cleyera gymnanthera,* &c.). In *Stuartia grandiflora* the cork-cells have thin walls. Sclerosed cells are intercalated as layers in the thin-walled cork of *Caraipa tereticaulis.* In *Kielmeyera tomentosa* the cork contains unsuberized cells with thin walls in addition to the typical cork-cells. Formation of phelloderm sometimes occurs in the Order, e.g. in *Haploclathra paniculata* and *Kielmeyera tomentosa,* in which the phelloderm is formed by cells thickened in the form of a U.

The pericycle either contains isolated groups of bast-fibres (species of *Cleyera* and *Gordonia*), or a ring of bast-fibres, or a composite and continuous sclerenchymatous ring (species of *Actinidia, Eurya, Freziera, Kielmeyera, Saurauja, Schima, Stachyurus, Ternstroemia, Visnea*). In the secondary bast only sclerenchyma in the form of rod-cells is known (in small amount in *Schima Kashiana*).

The **pith** has been accurately investigated only in species of *Stuartia* and in *Camellia japonica*, and in these plants it is reticulately heterogeneous. That is to say, the peripheral part of the pith consists of smaller active cells, the central part chiefly of larger, empty cells, but traversed by bands of active cells.

Sclerenchyma in the ground-tissue of the axis—in the pith and primary cortex—is of very wide-spread occurrence in the Order. The same different types of spicular cells, which were fully described above as occurring in the leaf-parenchyma, reappear in the ground-tissue of the axis in those species, which possess them in the leaf. Moreover, ordinary stone-cells or groups of them are also common in the ground-parenchyma of the axis in the Ternstroemiaceae. It may be mentioned that in *Actinidia* the peripheral part of the pith is formed by a cylinder of stone-cells, which encloses the inner thin-walled pith, and that in species of *Cleyera, Eurya, Freziera, Ternstroemia,* and *Visnea,* the stone-cells of the pith are arranged in the form of horizontal diaphragms.

Finally, the features presented by the secretions and crystals of the axis may be referred to. The secretory canals, which have already been shortly discussed under the leaf-structure, are only present in the genera of the Bonnetieae (excluding *Bonnetia*[1] and *Archytaea*), i.e. in *Kielmeyera, Caraipa, Mahurea, Marila,* and *Haploclathra.* According to Van Tieghem they are found in the branch either only in the pith and primary cortex (*Kielmeyera, Marila*), or in the outer part of the bast as well (*Caraipa, Mahurea, Haploclathra*—according to K. Müller in *Kielmeyera excelsa* also). The features presented by the crystals of the axis correspond to those of the leaf. In the Saurau jeae and Marcgravieae raphide-sacs are found in the axis, and elsewhere clustered crystals and ordinary solitary crystals. Hitzemann has observed sphaerocrystalline masses (gypsum?) in the pith of *Actinidia polygama.*

Anomalous structure of the axis does not occur (H. Schenck) even in the lianes belonging to the Order (*Actinidia* and species of *Marcgravia*).

Appendix: On the genus *Microsemma.*

The anomalous genus *Microsemma* (*M. salicifolia,* Labill. and *M. Balansae,* Baill.), which is placed by Bentham and Hooker at the end of the tribe Gordonieae, has recently been investigated by Van Tieghem with regard to its anatomical characters. The investigation showed that the appearance of sclerenchyma-fibres in the mesophyll recalls analogous features in the Ternstroemiaceae, but that the phloem-masses in the branch, which are narrowed outwards in the form of wedges, and are stratified into hard and soft bast, indicate an approach to the Tiliaceae. Passing to other characters, the following statements may be made regarding the anatomy of the genus. The stomata occur only on the lower surface of the leaf. Cork-formation takes place in the outermost cell-layer of the primary cortex of the branch. The cork-cells are flat and considerably thickened on their inner tangential walls. Fibrous sclerenchyma-cells are present in the primary cortex as well as in the leaf-tissue. The xylem has normal structure, and possesses uniseriate medullary rays. Oxalate of lime is excreted in the form of ordinary solitary crystals. The hairy covering of the branch consists of unicellular, hammer-shaped (i.e. two-armed ?), sclerotic hairs, the walls of which appear as though spirally thickened. As the genus in question has recently been referred by Baillon to the Thymelaeaceae, it may be pointed out that the vascular bundles are simply collateral in structure, which does not accord with classification among the Thymelaeaceae

Literature: Reinke, Sekretionsorg., Pringsheim Jahrb., Bd. x, 1876, p. 167.—Möller, Holzstr., Denkschr. Wiener Akad. 1876, pp. 81 and 377.—Molisch, Vergl. Anat. d. Ebenac. etc., Sitz.-Ber. Wiener Akad., Bd. lxxx, Abt. 1, 1879, p. 54 et seq.—Wittmack, Marcgrav., Verh. bot. Ver. Prov.

[1] K. Müller's statement, that a plant described by him as *Bonnetia tomentosa* possesses resin-canals, is to be explained by the fact that there is clearly a mistake in the naming of the genus as *Bonnetia* instead of *Kielmeyera* (with regard to this, see also Van Tieghem).

Brandenburg, Bd. xxi, 1879, p. 42.—E. Bachmann, Korkwuch., Pringsheim Jahrb., Bd. xii, 1879–81, pp. 194 and 205 et seq.—K. Müller, Engler, Bot. Jahrb., Bd. ii, 1881, p. 452 et seq.—Möller, Rindenanat., 1882, pp. 251.—Blenk, Flora 1884, p. 206 et seq., separate copy, pp. 36–40.—Van Tieghem, Bull. Soc bot. de France 1884, p. 148.—Mentovich, Mark, Klausenburg, 1885, Hungarian, abstract in Just 1885, i, p. 787.—Solereder, Holzstr., 1885, pp. 78–81.—Van Tieghem, Ann. sc. nat., sér. 7, t. i, 1885, pp. 43–6.—O. Bachmann, Schildh., Flora 1886, separate copy, p. 31.—Borzi, Alcune lenticelle fogliari, Malpighia i, 1886, p. 219 et seq. and Taf. v.—Hitzemann, Vergl. Anat. d. T. etc., Diss., Kiel, pp. 9–57 and 77–84.—Juel, Anat. d. Marcgraviac., Bihang K. Svenska Vetensk.-Akad. Handl., Bd. xii, 1887, abstract in Just 1887, ii; see also the same, Bot. Centralbl. 1888, i, p. 27.—Douliot, Périderme, Ann. sc. nat., sér. 7, t. x, 1889, pp. 336, 337.—J. E. Weiss, Korkbild., Denkschr. Regensb. bot. Gesellsch. 1890, separate copy, p. 66.—Szyszylowicz, in Naturl. Pflanzenfam., iii. Teil, Abt. 6, 1893, pp. 153, 158 and 176 et seq.—Gilg, in Natürl. Pflanzenfam., iii. Teil, Abt. 6, 1893, p. 193.—H. Schenck, Anat. d. Lianen, 1893, pp. 72, 73 and Tab. iii.—Van Tieghem, *Microsemma*, Ann. sc. nat., sér. 7, t. xvii, 1893, pp. 258–60.—Steppuhn, Vergl. Anat. d. Dilleniac., Diss., Bern, 1895.—Vesque, *Eurya*, Bull. Soc. bot. de France 1895, pp. 151–61.—Virchow, Blattzähne, Archiv der Pharm. 1896, p. 47 et seq.—[A. Richter, Z. phys.-anat. u. syst. Kenntn. d. Marcgravieen, etc., Természetrajzi Füzetek 1899, p. 27 and Tab. ii et seq. (Hungarian and German.)]

DIPTEROCARPEAE [1].

1. REVIEW OF THE ANATOMICAL FEATURES. For the diagnosis of the Order a series of excellent anatomical characters exists. Foremost among these is the possession of resin-canals, which occur in the pith and in the secondary wood. Secondly, the structure of the phloem, which recalls the well-known bast of the lime-tree; i.e. the bast-portions of the individual vascular bundles are narrowed outwards in the form of wedges in the transverse section of the branch, while the primary medullary rays (of the phloem) lying between them are broadened outwards like wedges to a corresponding extent; the phloem also consists of alternating layers of hard and soft bast. Further anatomical characters of the Order are: as regards the structure of the wood, the simple perforations of the vessels and the abundant development of wood-parenchyma; in the leaf, the almost universally bifacial leaf-structure and the vertically transcurrent smaller veins; the occurrence of vascular bundles in the primary cortex of the branch; lastly, the structure of the petiole and also of the midrib with a completely, or almost completely, closed annular system of vascular bundles, which surrounds a pith containing medullary bundles.

Oxalate of lime is usually developed in the form of clustered crystals, but also of ordinary solitary crystals. Mucilage-cells or mucilage-cavities occur not uncommonly in the primary cortex; further, one sometimes meets with mucilaginous epidermal cells in the leaf. The hairy covering consists of simple unicellular hairs, of tufted hairs and of variously shaped, glandular hairs. The latter (Fig. 31), in addition to a short stalk, either possess a disc-shaped, unicellular head lobed at the margin (*Dryobalanops*, *Hopea*, *Anisoptera*) or a 2–4-celled head, owing to the development of vertical walls (*Dryobalanops*, *Hopea*), or a scutiform head composed of a varying number of cells and having the structure of the well-known Oleaceous glands (*Anisoptera*, *Doona*, *Vateria*, *Shorea*).

For the diagnosis of the genera the following features may be made use of: the course of the cortical vascular bundles in the branch, the structural details of the vascular system in the petiole, and the position as well as the number of the resin-canals; likewise the pitting of the wood-prosenchyma, which is either simple or indistinctly bordered (*Vateria*, *Shorea*, *Hopea*) or typically bordered (*Dipterocarpus*, *Dryobalanops*, *Vatica*). Specific characters are found in the

[1] The three genera *Ancistrocladus*, *Lophira* and *Monotes*, referred to the Dipterocarpeae in Durand's Index, are excluded from the following description, and are discussed separately in an appendix to the Order.

occurrence or absence of mucilaginous epidermal cells in the leaf, in the appearance of sclerenchymatous fibres in the mesophyll, &c.

To conclude the general diagnosis, it remains to be mentioned that the stomata are sometimes, but not always, accompanied by special subsidiary cells, and regarding the origin of the cork, that the phellogen arises in the epidermis itself or in the outermost cell-layer of the primary cortex.

2. Structure of the Leaf. In the following statements on the leaf-structure I rely partly on Heim's work, but partly also on my own observations and on unpublished notes which Dr. O. Bachmann has placed at my disposal.

The leaves of the Dipterocarpeae are, as a rule, bifacial in structure. The **epidermal cells** have a small polygonal outline in surface-view. According to Heim the epidermal cells of the upper side of the leaf of *Pierrea* and *Dryobalanops* (including *Baillonodendron*) are characterized by their long (high) palisade-like form. Granulation of the cuticle is common; cuticular ridges have been observed by Bachmann in *Vatica lanceaefolia*, Bl. Gelatinization of the epidermis of the leaf is found in *Dipterocarpus geniculatus*, Vesque, according to Bachmann. The **stomata** are restricted to the lower surface of the leaf; they are, as a rule, surrounded by several ordinary epidermal cells, or by several cells differentiated more or less like subsidiary cells. Special subsidiary cells are known to me only in *Shorea robusta*, Gaertn. f., and *Richetia coriacea*, Heim; in the first species two subsidiary cells, in the second species one, are placed on each side of the pair of guard-cells, parallel to the pore. The medium-sized **veins** of the leaf are probably always vertically transcurrent, according to Bachmann and Heim; the tissue adjoining the vascular bundle of the vein on both sides or at any rate on the upper side consists, in most cases, of sclerenchyma-fibres; more rarely it is thin-walled. Sclerenchyma-fibres occur not only accompanying the vascular bundles of the veins, but sometimes also independently in the mesophyll; e.g., according to Bachmann, in *Vateria indica*, L. and *Hopea discolor*, Thw. **Oxalate of lime** occurs in the leaf (and likewise in the axis) principally in the form of clustered crystals, but accompanying them ordinary solitary crystals may occur. The resin-canals, which will be considered in greater detail in the discussion of the structure of the branch, are met with in almost all the members of the Order (exception: *Cotylelobiopsis*, Heim, see below) in the larger veins at the apex of the xylem-portions of the vascular bundles, but never free in the mesophyll. The **hairy covering** consists of clothing and glandular hairs. The clothing hairs are firstly simple, unicellular trichomes, which mostly have thick walls and narrow lumina; secondly, tufted hairs, composed of a varied number of unicellular hairs with thick walls and narrow lumina, or with less thickened walls and wider lumina. Among the external glands (Fig. 31) we may first mention the peltate glands, which are identical in their structure with the well-known Oleaceous type, and accordingly possess a disc-shaped, cellular plate of a varied number of cells, which in surface-view either meet at a central point or along a middle line (*Anisoptera lanceolata*, Walp., *Doona odorata*, Burck, *Monoporandra cordifolia*, Thw., *Pentacme suavis*, A. DC., *Shorea robusta*, Gaertn. f., *Vateria indica*, L.). With these peltate glands are connected those of *Parashorea stellata*, Kurz, the shield of which has less numerous cells and a margin which is somewhat lobed, not entire; and also the external glands of *Dryobalanops Beccarii*, Dyer, and *Hopea Beccariana*,

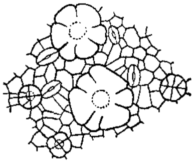

Fig. 31. Lower epidermis of the leaf of *Anisoptera lanceolata*, Wall.—Original.

Burck, with a 2–4-celled, discoid head; in the last-named of these species the glandular hairs are sunk in the epidermis of the leaf. Lastly, in certain members of the Order, in addition to the peltate Oleaceous glands, there are sometimes shortly stalked glands with a similarly disc-shaped, but unicellular head, which is more or less deeply lobed at its margin, e.g. in *Anisoptera lanceolata*, Walp., *Hopea Beccariana*, Burck, and *Dryobalanops Beccarii*, Dyer. In *Baillonodendron malayanum*, Heim, *Richetia coriacea*, Heim, and *Dipterocarpus Beccarii*, Dyer, I have not observed glandular hairs of any kind. To what extent the individual forms of the external glands are of importance in generic diagnosis still remains to be determined by the examination of more numerous species.

The **petioles** of the Dipterocarpeae have repeatedly formed the subject of thorough investigation by Burck, Pierre, Heim, and Brandis, with regard to the systematic significance of their structure. For the diagnosis of the Order, as shown by these investigations, prominence should firstly be given to the fact, that a closed ring of vascular bundles is always present in the petioles, or, at any rate, a ring that is not open at more than one point; this ring encloses a medullary, vascular bundle-system of varied and more or less complicated structure. The detailed composition of the vascular system of the petiole at the base of the lamina ('caractéristique' of French authors), the varying abundance of resin-canals on the inner side of the xylem-groups of the outer ring or arc of vascular bundles, and the absence, or the varied number, of resin-canals appearing in relation to the inner (medullary) bundle-system have been employed with success by the authors named for the diagnosis of the genera, as will be shown more fully by the conspectus of anatomical characters given at the end of the section on the axis.

3. Structure of the Axis. The following facts may be pointed out with regard to the structure of the **wood** on the basis of my investigations, which extended to species of the genera *Vateria*, *Dipterocarpus*, *Hopea*, *Dryobalanops*, *Vatica*, and *Shorea*. A transverse section of the wood shows mostly isolated vessels with round lumina and varying diameter (maximum ·07 to ·105 mm.) and rather broad, 3–5-seriate medullary rays. The vessels have simple perforations and on the walls, which are in contact with ray-parenchyma, they show transitions from typical bordered pits to simple pitting. The wood parenchyma is abundantly developed, as is especially conspicuous in *Vatica indica*, L., and *Shorea robusta*, Gaertn. f. In *Shorea robusta* the parenchyma-cells are occasionally septate and contain solitary crystals. In *Vateria*, *Shorea*, and *Hopea* the wood-prosenchyma possesses very small, often indistinct pit-borders; in *Dipterocarpus*, *Dryobalanops*, and *Vatica*, on the other hand, it shows typical bordered pitting. The more recent statement on this subject by Brandis and Gilg, according to which the pitting of the wood-prosenchyma is not constant for the genus *Dipterocarpus* (reference being made to *D. alatus*, Roxb. with distinct, and *D. tuberculatus*, Roxb. with very indistinct bordered pitting) requires further examination. According to Brandis, septation of the wood-prosenchyma occurs in *Pentacme*.

As regards the structure of the **cortex**, it may first be mentioned that, according to Heim, cork-formation takes place quite generally in a superficial position. Douliot observed the appearance of the phellogen in the epidermis of *Dryobalanops Camphora* and *Dipterocarpus nobilis*; Van Tieghem observed it in the subepidermal cell-layer in a plant described as *Dipterocarpus Bailloni*. Not uncommonly the primary cortex contains stone-cells, which are either uniformly thickened on all sides, or only on the inner tangential walls and the adjoining parts of the radial walls. Heim met with sclerosed parenchyma-cells of the second kind, the thickened walls of which appear in the form of a U in a transverse section of the branch, in species of *Dipterocarpus*, *Doona*,

Dryobalanops (incl. *Baillonodendron*), *Isoptera*, and *Shorea*. A further peculiarity of the primary cortex, appertaining only to some members of the Order, is the occurrence of cells with mucilaginous membrane, and of mucilage-cavities derived from groups of these cells. Mucilage-cavities and mucilage-cells of this kind have been observed by Heim and Brandis in species of the genera *Dipterocarpus*, *Doona*, *Richetia*, and *Shorea*. It may be noted that these structures sometimes also occur in the parenchyma of the petiole [1] in the genera named. The secondary cortex has a very characteristic structure. The phloem-portions of the individual vascular bundles, forming the bundle-ring, are narrowed outwards in the form of wedges in a transverse section of the stem; the parts of the primary medullary rays lying between these phloem-masses are correspondingly broadened outwards in the form of wedges. In addition to this the phloem-portions of the individual vascular bundles are stratified by means of tangential bands of hard bast in the same way as in the Lime. To judge by Heim's investigations, this structure of the bast is common to all the Dipterocarpeae.

The occurrence of **cortical vascular bundles** forms a further anatomical characteristic of the axis. In a transverse section the cortical bundles are either concentric or semilunar, they are accompanied by hard bast, and each of them possesses a resin-canal in connexion with its xylem-portion.

The cortical bundles in question originate in the following manner. Each leaf has three vascular bundles (leaf-traces), one median and two lateral. The median one usually (in all the genera except those named below) only separates from the bundle-ring of the axis at the node, while the lateral strands pass off from the bundle-ring earlier, at a lower level [2], as cortical bundles, as do also the vascular bundles belonging to the stipules, where stipules are present. The stipular bundles, however, are not always independent, but may branch off from the lateral leaf-traces. According to Brandis the genus *Stemonoporus*, and probably also *Vatica* and *Monoporandra*, forms an exception to the general type. In these cases the median leaf-trace leaves the bundle-ring far below the node and divides into 3–5 isolated bundles, which finally pass into the petiole. In these genera the lateral bundles leave the bundle-ring at a higher level and do not pass into the leaf, but only into the stipules.—The three bundles, which usually pass into the petiole, branch in the latter, as also do the resin-canals [3] accompanying them, in the most varied manner, and thereby bring about the differences presented by the appearance of the transverse section of the petiole (see above).

Lastly, mention may be made of the **resin-canals**, which are present in all the Dipterocarpeae (with the exception of *Lophira*, *Ancistrocladus*, and *Monotes*, see note on p. 136). In the axis they are found, in the first place, in the pith. They are present in the middle of the pith in the genus *Dryobalanops* only, which possesses a central resin-canal or a group of canals produced by division of the single one. In the rest of the Dipterocarpeae the resin-canals are found only in the peripheral part of the pith, and always in close relation to the xylem-portions of the vascular bundles of the bundle-ring, the connexion being sometimes so close that one is inclined to regard them as belonging to the primary wood, as indeed they were previously described by Van Tieghem. The number of these 'perimedullary' resin-canals varies. In *Dipterocarpus* their number amounts to 100; in the remaining genera 3–30 resin-canals are present; they vary not only in number but also in diameter. The balsam-canals occur

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[1] Secretory receptacles, possibly of a similar nature, are described by Heim in the following manner, for the petiole of the very incompletely known genus *Cotylelobiopsis*: 'Tout ce parenchyme est rempli de cavités, à contenu réfringent, bordées de cellules aplaties.'

[2] This takes place at different levels in the different genera; for this see the conspectus at the end of the structure of the axis.

[3] It is a rare occurrence for the three resin-canals to traverse the entire petiole (*Vatica obscura*, Trim. according to Brandis).

in the secondary wood as well as at the periphery of the pith. These interxylary resin-canals are mostly surrounded by wood-parenchyma, but sometimes by wood-prosenchyma, and they are often arranged in concentric circles; I have invariably met with them in the species enumerated in my 'Holzstruktur,' belonging to the genera *Vateria*, *Dipterocarpus*, *Hopea*, *Dryobalanops*, *Vatica*, and *Shorea*, and recently also in *Baillonodendron malayanum*, Heim, *Richetia coriacea*, Heim, and *Parashorea stellata*, Kurz. Their course has not yet been traced, nor their distribution in the Order. Regarding the latter point, it must be kept in view, that, according to Van Tieghem, the interxylary resin-canals sometimes do not appear until late in the secondary growth of the wood and hence cannot always be observed in branches from herbarium material; and further that, according to Leblois and Brandis, the resin-canals of the wood become filled up by means of a kind of tylosis-formation, as is the case with the resin-canals of *Brucea ferruginea* (Simarubaceae), &c., and consequently they may easily escape observation. The last-named phenomenon, moreover, occurs also in the perimedullary resin-canals. These latter pass out with the vascular bundles into the primary cortex and finally into the petiole and the veins of the leaf, and through their whole course retain the same position with regard to the xylem-groups as in the bundle-ring of the stem. Resin-canals completely independent of the vascular bundles are not present in this Order.

It is an interesting fact, that the resin-canals are already present in the embryo, accompanying the procambial strands [1] both in the plumule and in the cotyledons (in *Dipterocarpus turbinatus* and *Dryobalanops* according to Van Tieghem, and in *Doona* according to Brandis). The origin of the balsam-canals is schizo-lysigenous [2] according to the more recent developmental investigations made by Sieck in species of *Dipterocarpus*, *Doona*, *Dryobalanops*, *Isoptera* and *Vatica*. According to Brandis the contents of the resin-canals consist of balsam-like substances, which are liquid in the living plant, but in the air rapidly become converted into resin; the resin-canals, however, may also contain camphor-like substances, e.g. in *Dryobalanops aromatica*, Gaertn. f., the source of Borneo-camphor. The liquid contents, which are present in the living plant, and are obtained from species of *Dipterocarpus* as wood-oil, consist of an aromatic fluid, which is lighter than water, and as a rule fluorescent, and is mostly insoluble in alcohol and ether, but probably soluble in chloroform, carbon di-sulphide, and ethereal oils. It finally becomes resinous and is obtained as resin from many members of the Order. Lastly, it may be noted, that in the older wood the same substances as are contained in the resin-canals, are also present in the medullary rays, in the vessels and in the wood-parenchyma.

In connexion with the description of the structure of the axis there now follows a **synopsis** of the distribution of the resin-canals, of the course of the cortical vascular bundles and of the structure of the petiole at its upper end ('caractéristique'), features which have been made use of by Burck, Pierre, Heim, and Brandis for the anatomical diagnosis of the genera. With respect to these points it may be remarked that small divergences are sometimes to be found between the statements of the authors named, and that in the succeeding description I chiefly follow the most recent work of Brandis in the Journal of the Linnean Society, when not otherwise expressly stated, as Brandis was able to take into consideration the results of all the other authors. The serial succession of the genera in the following synopsis is that adopted by Brandis and Gilg for the revision of the Order (in 'Die natürlichen Pflanzenfamilien').

(1) *Dipterocarpus*, Gaertn. f. Pith with as many as 100 perimedullary resin-canals, sometimes in two circles. Of the three leaf-traces the two lateral ones pass into

[1] Heim moreover claims to have also observed independent resin-canals in the cotyledons of *Retinodendron* (= *Vatica*); see Heim, loc. cit., p. 23.

[2] Regarding this term, compare under Rutaceae.

the cortex at various levels, usually in the upper half of the internode; in the cortex there are also 7–12 stipular bundles. Petiole: peripheral bundle-system (*a*) consisting of a lower semicircle of 5–12 separate or connected vascular bundles, each provided with one resin-canal, and of an upper band of xylem and phloem (*b*) consisting, in *D. pilosus*, Roxb. only, of a closed bundle-ring; central bundle-mass with 1–8 resin-canals.

(2) *Anisoptera*, Korth. (incl. *Antherotriche*, Turcz.). Pith with 18–24 perimedullary resin-canals, the latter often rather large and close to one another. Of the three leaf-traces the two lateral strands run in the primary cortex through the entire internode in some of the species, through the upper half of the internode in the rest of the species. Petiole: peripheral bundle-system consisting of a closed ring of 7–13 bundles, the latter either (*Anisoptera Curtisii*, Dyer) separate, or fused, and provided each with one resin-canal; central bundle-mass without or with few resin-canals.

(3) *Dryobalanops*, Gaertn. f. (incl. *Baillonodendron*, Heim). At the base of the internode in the middle of the pith there is a single principal resin-canal. which higher up in the internode sends off branches, in order to furnish resin-canals for the leaf-traces of the next nigher leaf as well as for the bundles of the axillary bud; in *Dryobalanops oblongifolia*, Dyer, there are two principal canals according to Heim. Of the three leaf-traces the two lateral strands detach themselves from the bundle-ring at the base or in the middle of the internode. Petiole: peripheral bundle-system with five resin-canals, central bundle-system without resin-canals.

(4) *Doona*, Thw. Pith with 3–20 perimedullary resin-canals of unequal diameter, the larger canals three times as wide as the cells of the pith. Of the three leaf-traces the lateral strands, like the median trace, usually pass out from the bundle-ring only a short distance below the node, but in some cases in the upper third of the internode; each trace has one or sometimes 2–3 resin-canals; independent stipular bundles in the species with large stipules. Petiole: a semicircle of 3–11 usually connected bundles each with one resin-canal; central bundle-mass without or with a resin-canal.

(5) *Hopea*, Roxb. (incl. *Petalandra*, Hassk. and *Hancea*, Pierre). The anatomical features are very variable in *Hopea*, and to an extent found in no other Dipterocarpous genus.

(*a*) Section *Dryobalanoides*, Miq. (*Hancea*, Pierre). *Hopea cernua*, T. et B. shows at the base of the internode a triangular pith with three resin-canals in the angles; sometimes, owing to branching, a fourth resin-canal appears, and passes over into the leaf-trace of the next higher internode; of the three resin-canals first mentioned, two run through the whole length of the axis, while the third has branched off in the next lower internode and divides into five canals, of which two belong to the axillary bud, and three to the leaf. Burck states that of these three the two lateral canals with the corresponding leaf-traces do not enter the petiole, but belong to the stipules in the species of the section in question. Brandis is unable to confirm this in the case of *Hopea cernua*; but he states with certainty that in *H. Mengarawan*, Miq. and *H. Pierrei*, Hance, belonging to the same section, the third resin-canal mentioned above instead of dividing into five divides into a still larger number of canals (as many as eight), some of which belong to the axillary bud, the rest to the petiole. In all three species the lateral leaf-traces only separate from the bundle-ring immediately below the node. Petiole: *Hopea cernua* shows at the base of its petiole three isolated vascular bundles with one resin-canal each, besides a central bundle-mass without resin-canals; the upper end ('caractéristique') of the petiole is similar, except that the two lateral resin-canals have each divided into two. *H. Pierrei* resembles *H. cernua* in these respects. Lastly, *H. Mengarawan* has at the base of its petiole three isolated vascular bundles and five resin-canals; at the top of the petiole the central bundle-mass also contains three resin-canals.

(*b*) Section *Euhopea*, Miq., and *Petalandra*, Hassk. Number of the perimedullary resin-canals, which differ among themselves in diameter: 8–12 in *H. fagifolia*, Miq., *H. Recopei*, Pierre, *H. dealbata*, Hance, and *H. oblongifolia*, Dyer, according to Pierre, and in *H. odorata*, Roxb., and *H. glabra*, W. et A. according to Brandis, only 4 in *H. ferrea*, Pierre. As in the section *Dryobalanoides* the lateral leaf-traces run only for a short distance in the cortex; the resin-canal of the median trace divides into two, of which one passes into the axillary bud, the other into the leaf. The structure of the petiole differs essentially from that of the section *Dryobalanoides*, in that the number both of the vascular bundles and of the resin-canals in the peripheral bundle-system is greater.

(6) *Pentacme*, A. DC. Pith with 12–25 perimedullary resin-canals. The lateral leaf-traces pass out from the bundle-ring immediately below the node. Petiole with 7–9 vascular bundles in a semicircle and the same number of resin-canals; central bundle-mass with three resin-canals.

(7) *Shorea*, Roxb. (incl. *Parahopea*, Heim). Pith with 3–30 perimedullary resin-canals; resin-canals either with a small lumen (especially in some species of the section *Anthoshorea*), or with a wider lumen. Of the three leaf-traces the lateral ones separate from the bundle-ring at various levels: in *Shorea robusta*, Gaertn. f. in the middle of the internode, in *S. obtusa*, Wall. scarcely below the node; for *S. scaberrima*, Burck, *S. aptera*, Burck, *S. Pinanga*, Scheffer, *S. leprosula*, Miq. (*S. Maranti*, Burck) and *S. inappendiculata*, Burck, it is stated by Burck that the lateral leaf-traces with the resin-canals belonging to them run for 1½ internodes in the cortex; the consequence of this is naturally, that in the upper half of the internodes one meets with double the number (four) of lateral leaf-traces and of the resin-canals belonging to them. In species of *Shorea*, in addition to the cortical lateral leaf-traces, one also finds cortical stipular bundles with resin-canals, which either branch off from the bundle-ring, or from the lateral leaf-traces. The structure of the petiole varies; the characteristic region ('caractéristique') generally shows a semicircle composed of 7–9 isolated vascular bundles, each with one resin-canal, and a central bundle-system without resin-canals; in other species (*Shorea obtusa*) a bundle-ring and a central bundle-system without or with 1–3 resin-canals are found; in *S. robusta* 10–12 resin-canals occur both in the peripheral and in the central bundle-system.

(8) *Parashorea*, Kurz. Pith with 15 small peripherally-placed resin-canals. Cortical lateral leaf-traces only in the upper part of the internode. Petiole: peripheral semicircle of five vascular bundles, each with one resin-canal; central bundle-system without resin-canals.

(9) *Isoptera*, Scheffer (according to Pierre). Pith at the base of the internode with 16–18 canals. The lateral traces here also only leave the bundle-ring close to the node. Petiole: peripheral arc of bundles closed above by a band of wood and bast; numerous resin-canals also in the central bundle-system.

(10) *Balanocarpus*, Bedd. (incl. *Richetia*, Heim). (*a*) *Balanocarpus* (sensu Heim): Not very numerous resin-canals of unequal diameter at the periphery of the pith. Petiole with a peripheral arc of bundles; inner bundle-system of the petiole without resin-canals; (*b*) *Richetia*: 6–8 resin-canals at the periphery of the pith. Petiole: outer arc of bundles with 2–3 resin-canals, inner bundle-system without resin-canals. (Preceding statements according to Heim.)

(10 *a*) *Pierrea*, Heim[1]. Two resin-canals in the peripheral part of the pith at the base of the internode; higher up, as many as twelve canals owing to branching. The lateral leaf-traces enter the cortex in the upper third of the internode, the median trace in the uppermost fifth. Petiole: peripheral bundle-system with 12 resin-canals; inner system without any. (According to Heim.)

(11) *Cotylelobium*, Pierre (incl. *Dyerella*, Heim). In *Cotylelobium*, Pierre, numerous perimedullary resin-canals of large diameter in the axis. Petiole: peripheral bundle-system with large resin-canals; central bundle-system with no resin-canals (*Cotylelobium*) or with one (*Dyerella*). (Preceding statements according to Heim.)

(11 *a*) *Cotylelobiopsis*, Heim[1]. About 50 resin-canals at the periphery of the pith. Petiole even at its base without resin-canals. (Preceding statements according to Heim.)

(12) *Vatica*, L. (incl. *Pteranthera*, Bl., *Retinodendron*, Korth., *Isauxis*, Arn. and *Synaptea*, Griff.). Preliminary results: In the pith at the base of the internode 10–20 small peripheral resin-canals. The leaf-traces, as a rule, only pass out into the cortex immediately below the node. Petiole: peripheral bundle-system with 3–10 resin-canals, central bundle-system with few resin-canals or without any.

(13) *Pachynocarpus*, Hook. f. Agrees anatomically with *Vatica*.

(14) *Stemonoporus*, Thw. (incl. *Künckelia*, Heim, *Vesquella*, Heim, and *Sunapteopsis*, Heim). Pith with numerous (25–50) peripheral resin-canals, which are sometimes of unequal size, and may, in some cases, be of very large diameter. Of the three leaf-traces the median one leaves the bundle-ring at the middle of the internode, while the lateral strands do not branch off from the bundle-ring until close to

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[1] Based on incomplete material, and therefore not marked with a current number in the series.

the node and only pass into the stipules, not into the petiole; the median trace in its further course divides first into three, then into five bundles, which pass into the petiole. Petiole: bundle-system consisting of two peripheral arcs of bundles and of one central bundle-system; lower arc of bundles with 16 (*S. Wightii*, Thw.), 9–11 (*S. rigidus*, Thw., and *S. acuminatus*, Bedd.), or 13 (*S. reticulatus*, Thw.) resin-canals; upper arc of bundles in *S. Wightii* with 6 resin-canals; central bundle-system with 11 resin-canals (*S. Wightii*), or 2 (*S. rigidus* and *S. acuminatus*) or none at all (*S. reticulatus*).

(15) *Monoporandra*, Thw. Anatomically like *Stemonoporus* in essentials.

(16) *Vateria*, L. (incl. *Vateriopsis*, Heim). At the periphery of the pith, 25–60 resin-canals, which are of very unequal size and are abundantly branched. *Vateria Seychellarum*, Dyer, agrees with *Stemonoporus* in the course of its leaf-trace-bundles. Petiole: an external semicircle of vascular bundles with 10–15 resin-canals; central bundle-system, consisting of two flattened semi-lunar bundle-masses, with 3–7 large resin-canals.

4. Structure of the Root. In the roots of the Dipterocarpeae resin-canals are generally only present in the secondary wood. In a few species the perimedullary resin-canals of the hypocotyledonary stem extend into the uppermost part of the main root, which then contains a pith.

Appendix 1: *Ancistrocladus*.

The genus *Ancistrocladus*, which is referred to the Dipterocarpeae by Baillon and also by Bentham and Hooker, ranks more naturally as an independent Order, in accordance with its exomorphic and endomorphic characters, and had already been regarded as such by Planchon and A. de Candolle.

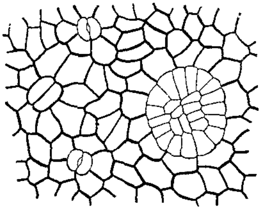

Fig. 32. Epidermis of lower side of leaf in *Ancistrocladus Heyneanus*, Wall.—Original.

In this genus resin-canals are absent in pith, wood and cortex. Van Tieghem's statement as to their occurrence in the pericycle is, according to Heim, Gilg and my own investigation (the latter in *A. extensus*, Wall., and *A. Heyneanus*, Wall.), incorrect and consequently also Van Tieghem's speculation with regard to the systematic position of the genus. Cork-formation takes place at various depths in the primary cortex (e.g. in the second and third cell-layer from the outside in *A. Vahlii*, near the pericycle in *A. guineensis*) and is frequently accompanied by development of phelloderm. Hard bast is usually wanting in the pericycle (*A. Heyneanus*), or small bundles of hard bast are present (*A. extensus*). The features characteristic of the bast of the Dipterocarpeae, viz. its form in transverse section and the stratification into hard and soft bast, are not present. The secondary bast and sometimes also the primary cortical tissue, however, contain stone-cells, which are more or less branched, and in the secondary bast are often elongated in the vertical direction, and which in their form recall *Cinchona*-sclerenchyma (*A. extensus* and *A. Heyneanus*).

As regards the structure of the wood, in *A. extensus* I find narrow medullary rays, scattered vessels with lumina of medium size, and with simple perforations and bordered pits even in contact with the parenchyma of the medullary rays, rather thick-walled wood-prosenchyma with bordered pits (according to Gilg also) and tangential bands of wood-parenchyma in the later growth of the wood.

According to Heim and Gilg, and I am able to confirm this in the case of *A. extensus*, peculiar clustered and solitary crystals consisting of oxalate of lime occur in the pith and cortex of the branch. The former resemble sphaerites; the latter differ from ordinary solitary crystals in having a more rod-like shape and a somewhat corroded surface.

The leaf, in the two species investigated by me, is characterized especially by the possession of vertically transcurrent veins and of peltate hairs (Fig. 32) of characteristic structure. The latter are of medium size, are visible even to the naked eye,

and do not cause any dense covering on the leaf-surface. The stalk consists of a small cell-plate, which is formed by 2–4 thick-walled cells; the shield has an entire margin and is composed of a layer of cells, which have a polygonal outline in surface-view, and, in their arrangement, indicate more or less clearly the original division of the mother-cell of the shield into four cells. Each of the stomata is surrounded by several ordinary epidermal cells.

2. *Lophira*.

The genus *Lophira* included among the Dipterocarpeae by Bentham and Hooker and others, but recently appended to the Ochnaceae by Gilg, deviates anatomically from the previous Order according to Van Tieghem. In *L. alata*, Banks, the stratification of the bast peculiar to the Dipterocarpeae is, in the first place, wanting; in the pericycle isolated groups of hard bast are present, while secondary hard bast is absent. Secondly, resin-canals are not developed. Thirdly, the petiole is differently constituted from that of the Dipterocarpeae; for it contains isolated vascular bundles. On the other hand, in common with the Dipterocarpeae, *Lophira* has cortical bundles (according to Douliot), superficial cork-formation, and also (according to Cas. de Candolle) the same type of structure in the midrib of its leaf.

In completion of the anatomical diagnosis of *Lophira*, it may be added that, according to Van Tieghem, isolated sclerenchyma-fibres or groups of these elements occur in the pith and primary cortex, and that, according to Heim, the leaf-structure is bifacial, that a one-layered hypoderm is developed below the upper epidermis, that the stomata occur only on the lower side and are accompanied by two subsidiary cells, which are parallel to the pore, and that oxalate of lime is excreted in the form of clustered crystals.

3. *Monotes*.

The genus *Monotes* is separated from the Dipterocarpeae by Brandis and Heim on account of its exomorphic features (short androgynophore) and the absence of resin-canals. Heim regards the genus as an intermediate type between the Dipterocarpeae and the Tiliaceae.

In place of resin-canals, as in certain Dipterocarpeae and Tiliaceae, numerous mucilage spaces are found in the pith, primary cortex, and bast of *Monotes*; these are approximately isodiametric or are elongated in the vertical direction; in the primary cortex they are provided with a distinct epithelium, though they are lysigenous throughout. An approximation to the Dipterocarpeae in anatomical characters is afforded by the following features: the three leaf-traces and the occurrence of cortical bundles, owing to the lateral leaf-traces running in the primary cortex through almost the entire internode; the occurrence of numerous parenchymatous sclerenchyma-cells in the primary cortex of the axis; the excretion of oxalate of lime in the form of clustered crystals; and lastly the stomata, each of which is surrounded by several epidermal cells. On the other hand, the characteristic form of the groups of bast in the bundle-ring of the axis appertaining to the Dipterocarpeae and Tiliaceae is wanting in *Monotes*. The bast, however, is stratified. The pericycle contains an almost continuous ring of fibres; the secondary bast contains concentric sclerenchymatous rings, which consist of secondary hard bast and sclerosed ray-parenchyma. In *Monotes* the hairy covering consists of rather long simple unicellular trichomes, which are often somewhat tortuous, of rather shorter unicellular hairs grouped in tufts, and of glandular hairs (the last being either shortly stalked with a unicellular spherical or ellipsoid head, or club-shaped, but even then uniseriate).

To complete the diagnosis I add the following statements, in accordance with what is found in Mechow's specimen No. 434: the leaf-structure is centric, the whole of the mesophyll being formed of palisade-tissue which becomes looser towards the lower side; there is a 1–2-layered hypoderm below the upper epidermis of the leaf (*while Heim figures bifacial structure* and *no hypoderm in the plant investigated* by him); the hypoderm and the strikingly small-celled lower epidermis contain cells with mucilaginous membranes.

Literature: Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 80, 81, and 376.—Cas. de Candolle, Anat. comp. des feuilles, Mém. Soc. de phys. et d'hist. nat. de Genève, t. xxvi, 2, 1879, pp. 440, 441, pl. ii.—K. Müller, Engler, Bot. Jahrb., Bd. ii, 1882, pp. 446–51.—Van Tieghem, Bull. Soc. bot. de France, 1884, pp. 141 and 392 et seq.—Solereder, Holzstr., 1885, pp. 81–3.—Van Tieghem, Ann. sc. nat., sér. 7, t. i, 1885, pp. 27, 59 and 67 et seq.—Hitzemann, Vergl. Anat. der D. &c., Diss.

Kiel, 1886, pp. 84-92.—Burck, D. des Indes néerl., Ann. Jard. bot. de Buitenzorg, vol. vi, 1887, p. 145 et seq.—(Leblois, Canaux sécrét., Thèse, Paris, 1888).—Van Tieghem, Ann. sc. nat., sér. 7, t. viii, 1888, p. 142 et seq.—Douliot, Ann. sc. nat., sér. 7, t. x, 1889, p. 342, 343.—Pierre, Flore forest. de la Cochinchine, Fasc. xvi, xvii, tab. 250–7, 1891–2.—Van Tieghem, Can. sécrét. dans les D., Journal de bot. 1891, pp. 378–85.—Heim, *Ancistrocladus*, Bull. Soc. Linn. de Paris, 1892, pp. 1059–61 and Rech. sur les D., Thèse, Paris, 1892, 186 pp. and 11 pl.—Becheraz, Sekretbild., Diss., Bern, 1893, p. 30 et seq.—Gilg, Ochnaceae, in Natürl. Pflanzenfam., 3. Teil, Abt. 6, 1893, p. 134 and Ber. deutsch. bot. Gesellsch., 1893, p. 20 et seq., as also Ancistrocladaceae, in Natürl. Pflanzenfam., loc. cit., 1894, pp. 274, 275.—Brandis and Gilg, in Natürl. Pflanzenfam., 3. Teil, Abt. 6, 1895, pp. 244–8.—Sieck, Sekretbeh., Pringsheim Jahrb., Bd. xxvii, 1895, p. 231 et seq.—Brandis, Enum. of the D., &c., Journ. Linn. Soc., vol. xxxi, 1895, pp. 1–148, and 3 pl., especially pl. 1.—[Poulsen, Nektarier, Vidensk. Meddelels. fra naturh. For. i Kjøbenhavn, 1897, pp. 356–71, 3 tab.]

CHLAENACEAE.

Only a few statements[1] have been published on the anatomy of this small Order, which is endemic for Madagascar. In addition to these, a casual investigation of my own on the leaf-structure of *Sarcolaena multiflora*, Thouars, *Leptolaena multiflora*, Thouars, *Schizolaena rosea*, Thouars, and *Rhodolaena* sp. Hildebrandt n. 3823, is taken into consideration in the following description.

The leaf is bifacial in structure. The **epidermal cells** on both sides of the leaf have a polygonal contour, and are characterized by their small dimen-

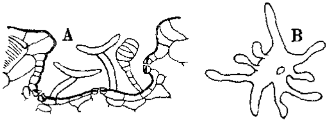

Fig. 33. A, Transverse section through one of the small depressions (pits) on the lower surface of the leaf of *Schizolaena rosea*, Thouars. B, Small scale of *Sarcolaena multiflora*, Thouars in surface-view.—Original.

sions in *Sarcolaena multiflora* (on the upper side) and in *Rhodolaena* sp. (on both sides). In *Sarcolaena multiflora*, *Schizolaena rosea*, and *Rhodolaena* sp., the integumental tissue of the upper side of the leaf is strengthened by the development of a 1–2-layered **hypoderm**. The latter, in *Sarcolaena multiflora* and *Schizolaena rosea*, contains cells with mucilaginous inner membranes, while in *Leptolaena multiflora* similar cells are present in both upper and lower epidermis and in this plant penetrate deep into the mesophyll. The **stomata** are surrounded by a rather large number of ordinary epidermal cells. They occur only on the lower side of the leaf, and are uniformly distributed over it in *Leptolaena* and *Rhodolaena*, while in *Sarcolaena* and *Schizolaena* they are restricted to small depressions on this surface (Fig. 33). The vascular bundles of the **veins** are always accompanied by sclerenchyma. They are either embedded in the mesophyll (*Leptolaena*) or are vertically transcurrent (*Sarcolaena, Schizolaena, Rhodolaena*). In the latter case the vein is either (*Sarcolaena, Schizolaena*) transcurrent on the upper side by means of plates of sclerenchyma, while parenchymatous tissue, having large lumina and sometimes containing mucilage-cells, adjoins the vascular bundle on the lower side, or (*Rhodolaena*) it is vertically transcurrent on both sides by means of lignified parenchyma.

[1] Literature: Solereder, Holzstr., 1885, p. 83.—Van Tieghem, Ann. sc. nat., sér. 7, t. i, 1885, p. 75, note.—Hitzemann, Diss., Kiel, 1886, pp. 92–4.—K. Schumann, Natürl. Pflanzenfam., 3. Teil, Abt. 6, 1893, pp. 168–9.

The **hairy covering** (Fig. 33) consists of clothing and glandular hairs. The clothing hairs are either (*a*) ordinary simple unicellular trichomes with thick walls and narrow lumina, as a rule compressed at the base, not much elongated, and pointed at their ends (branches of *Rhodolaena*); or (*b*) two-armed unicellular hairs, with thick walls and narrow lumina, and with arms which are usually of very unequal length and often curiously twisted (leaves and parts of the flower of *Sarcolaena*, *Schizolaena* and *Leptolaena*, and, according to Schumann, in *Xerochlamys* also); or lastly, (*c*) peltate hairs (small pits in the leaf of *Sarcolaena* and *Schizolaena* and parts of the flower of *Leptolaena*), which consist of a unicellular thin-walled shield with more or less numerous rays, and of a unicellular or multicellular stalk, which is often elongated. The glandular hairs are multicellular and either club-shaped or stalked, being provided in the latter case with an ellipsoid few-celled head.

The following is to be noted with regard to the structure of the branch. A transverse section of the **wood** (*Sarcolaena*, *Leptolaena*) shows 1–2-seriate medullary rays and mostly isolated vessels with rather small lumina (maximum diameter, ·048 mm.). The vessels have *simple perforations*, and, where they are in contact with parenchyma of the medullary rays, they bear bordered pits with transitions to large simple elliptical pits. Here and there the wood-parenchyma is abundantly developed. The wood-prosenchyma has thick walls, and rather narrow lumina, and bears typical bordered pits on its walls.

The **pith** of *Sarcolaena multiflora* and *Leptolaena multiflora*, and likewise, according to Schumann, of *Xerochlamys pilosa*, Baker[1], contains mucilage-spaces formed by cells, the membranes of which are mucilaginous on all sides or on one side only; in *Sarcolaena multiflora* similar elements are also present in the primary cortex. Moreover, stone-cells have been observed in the pith and primary cortex in *Sarcolaena multiflora*. The pericycle (*Sarcolaena*, *Leptolaena*, *Rhodolaena*) contains isolated groups of bast-fibres, and the secondary bast contains bands of bast-fibres, which are sometimes united by sclerosed ray-parenchyma.

Oxalate of lime is excreted in branch and leaf in the form of clustered crystals.

MALVACEAE.

1. Review of the Anatomical Features. The Malvaceae are characterized by the possession of stellate hairs, of secretory organs containing mucilage, and of bast with a characteristic structure, although these three anatomical features do not appear in every member of the Order. The mucilage-containing secretory organs are either (*a*) epidermal cells, which have a mucilaginous inner membrane and frequently give rise to transparent dots in the leaf, or (*b*) cells with mucilaginous walls in the ground-tissue of axis and leaf, or (*c*) mucilage-cavities of lysigenous origin, which are sometimes differentiated as canals. In a transverse section of the branch the phloem-portions of the vascular bundles have a wedge-shaped contour, which narrows outwards, while conversely the primary medullary phloem-rays lying between them become broader outwards; the bast-portions are, moreover, stratified into hard and soft bast.

The leaves of the Malvaceae are almost always bifacial in structure; embedded as well as vertically transcurrent veins occur; a special type of stoma is not present; in certain species sclerenchymatous elements are present in the mesophyll (*Bombax*, *Goethea*, and *Pavonia*) and stomata occur on both sides of the leaf. The structure of the axis shows uniformity as regards the occurrence of simple perforations in the vessels and the lack of wood-prosen-

[1] K. Schumann's citation '*X. multiflora*, Bak.' is probably only an oversight.

chyma with typical bordered pits. The medullary rays of the wood vary in breadth; wood-parenchyma is either abundant or scant; the wood-prosenchyma either has thick walls and narrow lumina or has broad lumina. The cork arises in the outermost cell-layer of the primary cortex or in the epidermis.

The hairy covering (Fig. 34), apart from the stellate hairs already mentioned, consists of simple, unicellular or uniseriate bristle-hairs, and of peltate and glandular hairs of varied structure. Oxalate of lime is deposited in the form of ordinary solitary or clustered crystals. Lastly, in some members of the Order (*Gossypium, Fugosia, Thespesia*) there are schizogenous (?) secretory cavities, which are filled with brown contents, and are frequently to be observed even with the naked eye as opaque or transparent dots in the leaf, &c.

2. Structure of the Leaf[1]. According to the investigations of G. Kuntze and Dumont the leaves of the Malvaceae are almost always bifacial in structure. Centric structure has only been observed in *Chorisia crispiflora*, by Dumont, and in *Malva parviflora*, L., by Volkens. The **epidermal cells** have straight or undulated lateral walls. A many-layered epidermis has only been met with in three species (*Gossypium drynarioides, Bombax pubescens*, and *Durio zibethinus*). Occasionally only a certain number of the epidermal cells are divided by horizontal walls into two cells, e.g. in *Chorisia asperifolia*, St. Hil., and *Quararibea floribunda*, K. Schum. Hypoderm is described by Radlkofer in *Durio lanceolatus*, Mast. The cuticle varies very much in thickness; thus in the Hibisceae and Althaceae it is thin; in most of the Bombaceae thicker, while in *Bombax pubescens*, Mart., it is very thick and strong, besides being provided with a coating of wax. Striation of the cuticle is of frequent occurrence; high cuticular ridges are, however, found only in *Pachira aquatica, Ceiba Rivieri*, K. Schum., *C. erianthus*, K. Schum., *Carolinea alba*, Lodd., and *Chorisia insignis*, H. B. K. The occurrence of cells with mucilaginous membranes in both upper and lower epidermis is a very wide-spread phenomenon in the Order. These cells are found especially in the upper epidermis, where they are often of considerable size, and in that case their inner portions penetrate the mesophyll, e.g. in *Althaea rosea*, Cav., *Pavonia monatherica*, Cas., several species of *Malvaviscus*, all the Hibisceae and *Adansonia* according to Kuntze, and in species of *Durio* and *Boschia* according to Radlkofer; in these latter, the large mucilaginous epidermal cells are flask-shaped and cause transparent dots in the leaf. In the development of the **stomata**, according to Dumont an epidermal cell divides once, twice, or three times; the cell last separated becomes the mother-cell of the two guard-cells. Consequently, the guard-cells in this Order are surrounded by a variable number of epidermal cells, and hence the stomatal apparatus presents a constant anatomical character only in so far as special subsidiary cells are wanting. In the Ureneae and Bombaceae, according to Kuntze's statements, the stomata are present only on the lower surface of the leaf; in the remainder of the Malvaceae, according to the same author, stomata are as a rule also present in the upper epidermis when the leaf is densely covered with hairs on its upper side. Malformed stomata occur in large numbers in *Thespesia populnea*, Corr. According to the investigations of Kuntze, the smaller **veins** are vertically transcurrent or embedded; embedded veins were observed in some of the Malveae, in the Ureneae and Hibisceae, vertically transcurrent veins in the Malveae and in the Bombaceae. Sclerenchyma may occur accompanying the vascular bundles (in the Malveae rarely, e.g. in *Kydia calycina*, Roxb., and *Hoheria populnea*, A. Cunn., where only

[1] Most important literature: Dumont, 1887, and Kuntze, 1891, ll. cc. The genera investigated by Dumont are enumerated below in the description of the mucilage-receptacles; with regard to the material investigated by Kuntze, see the work of that author.

two or three bast-fibres are present; further, in most of the Ureneae and Hibisceae as well as in the majority of the Bombaceae), or it may be absent (in most of the Malveae, in *Senra incana*, Cav., *Hibiscus diversifolius*, Jacq., *Gossypium herbaceum*, L., in *Adansonia* and *Ochroma*). Sclerenchymatous elements, running freely in the mesophyll, are stated by Kuntze to occur in the form of fibre-like cells in *Bombax pubescens*, *Goethea coccinea*, and *Pavonia intermedia*.

The structure of the principal vein is often complex in the Bombaceae, according to Kuntze. Transitions to this complex type occur in representatives of the remaining tribes. For details on this point, Kuntze's work should be referred to.

Regarding the **petiole**, it may be mentioned that in the Bombaceae, and in species of *Abutilon*, *Anoda*, *Hibiscus*, and *Lavatera*, a transverse section exhibits an uninterrupted ring of wood, while in other Malvaceae the petiole is traversed by isolated vascular bundles embedded in the ground-tissue. The number of the bundles varies, and does not agree even in the most closely related species of the same genus. According to Kuntze and Dumont (ll. cc.), the fibro-vascular system in the petioles of *Bombax pubescens*, Mart., *Durio zibethinus* and of *Coelostegia*, possesses a very complicated structure.

To complete the description of the leaf-structure, some anatomical features appertaining to the axis as well as to the leaf, viz. the secretory organs, the features of the crystals and the hairy covering, may be reviewed. The **mucilaginous contents** of the epidermis of the leaf in many species has already been discussed above. In the members of this Order, mucilage however also occurs elsewhere, in the axis as well as in the leaf, and always originates by metamorphosis of the cell-wall [1]. The mucilage-receptacles are either cells or spaces of lysigenous origin, which are sometimes of the nature of canals.

Dumont makes a series of very valuable statements on the occurrence and distribution of the mucilage-containing elements in the axis and leaf. Below I will only give quite a short abstract of these statements, and refer to the original treatise for further particulars. We cannot here enter into the detailed statements of Kuntze and Walliczek, dealing with the same features.

Dumont, in the first place, describes mucilage-cells and mucilage-cavities as occurring in the axis (pith and cortex) of the Eumalveae (*Malva*, *Althaea*, *Lavatera*, *Napaea*), Sideae (*Anoda*, *Sida*, *Cristaria*, *Hoheria*), and Malopeae (*Kitaibelia*, *Malope*, and *Palava*) investigated by him. In the Sideae only a few mucilage-cells are present in the pith; they here become united into short lysigenous canals. Still more elongated mucilage-canals are found in the pith of the Malopeae. In the Abutileae (*Abutilon*, *Wissadula*, *Sphaeralcea*, *Kydia*), in the Ureneae (*Urena*, *Pavonia*, *Malvaviscus*, *Goethea*, *Malachra*), and in the Hibisceae (*Hibiscus*, *Lagunaria*, *Gossypium*, *Thespesia*, *Fugosia*) the number of mucilage-cells and mucilage-cavities is much smaller than in the Eumalveae, &c. In the Abutileae, Ureneae, and Hibisceae canal-like mucilage-cavities, which correspond to those of the Malopeae, appear in *Malachra* and *Hibiscus* only. Lastly, in the tribe Bombaceae, the Adansonieae (*Eriodendron*, *Bombax*, *Adansonia*, *Chorisia*, *Pachira*) possess mucilage-cells and mucilage-cavities in abundance; these are rare in the Matisieae (*Quararibea*, *Ochroma*, *Scleronema*, *Hampea*), very rare in the Durioneae (*Durio*, *Coelostegia*, *Boschia*). In the three genera of the Durioneae last mentioned canal-like mucilage-cavities are present in the pith. Before leaving the subject of the mucilage-elements of the axis, the occurrence of these elements in the wood- and bast-parenchyma of the roots of *Althaea* and *Napaea* deserves special mention.

In the leaves, according to Kuntze, apart from the epidermis, mucilage is frequently found in elongated canals on the lower side of the vascular bundles of the veins. Mucilage-receptacles also occur in the mesophyll, e.g. mucilage-

[1] Hartwich's statement (Hartwich, loc. cit.) that the mucilage of the marsh-mallow is a direct product of the protoplasm is incorrect.

cells in *Plagianthus sidoides*, Hook., *Hoheria populnea*, A. Cunn., *Quararibea turbinata*, Poir. (Radlkofer).

Secretory cavities, filled with brown contents, must not be confused with the mucilage-receptacles. They occur in the closely allied genera *Gossypium*, *Thespesia*, and *Fugosia*, and, according to Dumont, are of schizogenous origin[1]. They cause translucent or dark opaque dots in the foliage-leaves, sepals, &c.

Oxalate of lime is excreted in the form of ordinary solitary or clustered crystals. Bodies resembling crystals, of unknown chemical composition, and consisting of numerous raphide-like needles, are, according to Kuntze, found in the epidermal cells of *Goethea coccinea*.

The types of **hairs** in this Order are very diverse, embracing stellate hairs, tufted hairs, small scales, simple bristle-hairs, and glandular hairs of various

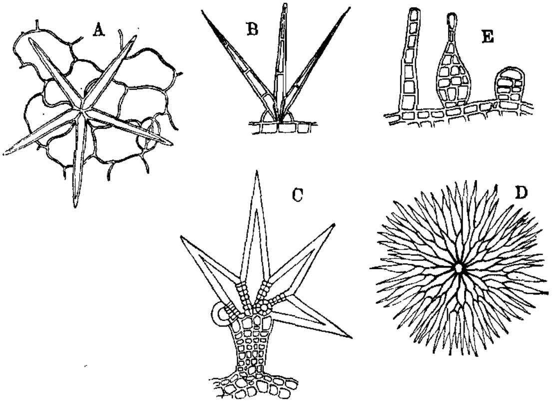

FIG. 34. Hairy covering of the Malvaceae. A, Stellate hair of *Althaea officinalis*, L. B, Stellate hair of *Malachra radiata*, L. C, Stellate hair of *Malvastrum asperrimum*, Garcke. D, Peltate hair of *Durio lanceolatus*, Mast. E, Hairy covering of *Malvastrum capense*, Gray.—A, After Vogl; B–C and E, after Kuntze; D, after O. Bachmann.

shapes. Several of these sometimes occur in one and the same species. The stellate and tufted hairs (Fig. 34, *A–C*) are to be regarded as the characteristic form of hair in the Order, on account of their wide distribution in it. Different forms of stellate hairs depending on the number, length, arrangement, and insertion of the ray-cells are found, but cannot be more fully described here. I will only mention that the stellate hairs are sometimes seated on multiseriate emergences (Fig. 34, *C*) and that in *Malachra radiata*, L. (Fig. 34, *B*), according to Kuntze, the rays are not unicellular as is usually the case, but uniseriate.

The peltate hairs have been investigated by O. Bachmann in species of *Thespesia*, *Hibiscus*, *Boschia*, *Durio*, and *Neesia*. Kuntze, moreover, states that peltate hairs occur also in *Plagianthus squamatus*, Benth., and in *Bombax*

[1] According to Höhnel, the origin of the secretory cavities in the cotyledons of *Gossypium herbaceum* and in the capsular fruits of '*Thespesia malvacea*' is lysigenous.

pubescens, Mart.; according to Dumont, they are found in '*Lagunea squamea*' (= *Hibiscus* sp.) and *Coelostegia Griffithii*, and according to K. Schumann in all the genera of his group Durioneae (i. e. in *Cumingia, Camptostemon, Durio, Dialycarpa, Neesia, Boschia, Coelostegia*, and *Cullenia*) and in species of *Quararibea*. The peltate hairs, investigated in detail by Bachmann, show three types of structure. The first form, which occurs in the genus *Thespesia*, presents no special peculiarity; its ray-cells are thin-walled, pointed at their ends, and almost completely united. The peltate hairs of *Hibiscus Patersonii*, Ait., on the other hand, are characterized by the possession of a 'small upper scale'; the ray-cells here have fairly thick walls, run out to a point, and are united with one another for unequal distances. The third form (Fig. 34, *D*) is represented in the genera of Bombaceae by peltate hairs, in which the shield exhibits a more or less pronounced doubling in the radial direction, inasmuch as the ray-cells extending outwards from the centre of the shield mostly stop short of the margin, while those forming the margin do not reach the centre, so that the marginal cells form, as it were, a frame round the central cells, which in themselves are already united to form a small scale. It may be added that the bristle-shaped hairs are either unicellular or uniseriate.

Lastly, the glandular hairs (Fig. 34, *E*) are of various forms, according to Kuntze. Small unicellular or few-celled glandular hairs, frequently enclosed in depressions of the epidermis, occur in species of *Althaea, Hibiscus, Malva*, and *Pavonia*. In species of *Abutilon*, in *Hibiscus setosus*, and *H. splendens*, for example, they are formed by a filament of cells, of which the uppermost cell is somewhat enlarged. The glandular hairs of *Cristaria andicola*, Gay consist of a very long basal cell, followed by two or three very small cells and then a large cell forming the head. Multicellular, glandular hairs, which are spherical, pitcher-shaped, or flask-shaped, are of freqnent occurrence in species of *Malva, Malvastrum*, and *Wissadula*. Finally, the depressed glandular hairs of *Adansonia* and of *Althaea officinalis*, L., also deserve mention. In section they exhibit a basal cell, a disc-shaped stalk-cell, and a tier of elongated cells arranged in the form of a fan; seen from above, these hairs have the appearance of ordinary many-celled glandular hairs.

Extra-floral nectaries occur as depressed callosities of the midrib on the lower side of the leaf in species of *Hibiscus, Urena*, and *Gossypium*. In *H. tiliaceus*, L. they consist essentially of a pit, which is often deep, with a number of recesses, and is provided with a narrow orifice, while the basal surface of the pit is beset with multicellular glandular hairs (Delpino).

3. Structure of the Axis. To begin with the structure of the **wood**, the following features may be specially pointed out, as shown by my own investigations, which extended to species of the genera *Plagianthus, Hoheria, Pavonia, Malvaviscus, Hibiscus, Thespesia, Adansonia*, and *Neesia*. The medullary rays of the wood vary in breadth; thus they are as much as 9-seriate in *Hoheria populnea*, A. Cunn., as much as 3-seriate in *Malvaviscus arboreus*, Cav., and *Thespesia populnea*, Corr. The arrangement of the vessels and the size of their lumina also show diversity; the maximum diameter varies between ·036 mm. (*Plagianthus sidoides*, Hook.) and ·105 mm. (*Adansonia*). The vessels, where they are in contact with one another, have bordered pits of varied size (diameter of the border = ·003–·006 mm.). On the vessel-walls, which are in contact with parenchyma of the medullary rays, either bordered pits are present or simple pits with transitions to the former; the last-mentioned character of the vessel-wall is peculiar to the genera *Adansonia, Hoheria*, and *Plagianthus*. Spiral thickening of the vessel-wall has been described by me in *Hoheria populnea*, A. Cunn. and *Plagianthus sidoides*, Hook., and by Möller in *Sida pulchella*, Bonpl. The perforations of the vessels are simple. The wood-parenchyma is sometimes abundant, e.g. in *Adansonia, Durio, Neesia*, but scanty in *Pavonia*.

The wood-prosenchyma has lumina of varying width; it either has thick walls and narrow lumina, as in *Plagianthus*, or wide lumina, as in *Malvaviscus*; the walls are provided with pits which are simple, or have a small and indistinct border. Septation of the wood-prosenchyma occurs in *Adansonia* [1].

I have recently observed an extremely noteworthy anatomical feature in the structure of the medullary rays of the wood in *Durio lanceolatus*, Mast., *Boschia acutifolia*, Mast., and *Neesia purpurascens*, Becc. These rays exhibit tiers of cells; the latter are brick-shaped and are placed with their greatest dimension in the vertical direction, and with their next largest dimension in the tangential direction, so that, in a transverse section of the branch, they are elongated in the tangential, and not, as is usually the case, in the radial direction, while in a radial longitudinal section they are distinguished from the other cells of the medullary ray by their slight breadth and considerable elongation in the vertical direction.

According to Höhnel, the wood of the stem of *Thespesia populnea*, Corr., possesses well-marked tiers in its medullary rays.

Regarding the **pith**, mention may be made of the occurrence of stone-cells in *Matisia ochrocalyx*, K. Schum. according to Kuntze, and of sclerenchyma-fibres resembling hard bast on the inner side of the wood in *Plagianthus sidoides*, Hook., and *Hoheria populnea*, A. Cunn. according to my own observations; and in *Hibiscus setosus* and *Bombax malabaricum*, DC. according to those of Kuntze. The pith of the species of *Hibiscus* is homogeneous according to Mentovich.

With regard to the **cortex**, the origin of the cork deserves special mention. According to Dumont and others, it arises in the outermost cell-layer of the primary cortex in most cases. The following are the only exceptions, according to Dumont: the majority of the Ureneae, almost all the species of *Hibiscus*, and lastly, *Sida pulchella*, in which the epidermis becomes the phellogen.

Three zones may usually be distinguished in the primary cortex. The outermost is parenchymatous, and is not very thick; according to Dumont, mucilage-receptacles occur here in the Eumalveae only. The middle zone is collenchymatous; the innermost is parenchymatous, and is, as a rule, the seat of formation of the mucilage-elements. In a large number of the Bombaceae, e.g. in *Boschia acutifolia*, Mast., a ring of stone-cells is present in the primary cortex. Stone-cells, according to Kuntze, also occur in the cortex of *Pavonia intermedia* and *Goethea coccinea*.

The **bast-portions** of the vascular bundles always possess the same characteristic type of structure, recalling that of the bast of the lime. That is to say, in a transverse section of the branch they are narrowed outwards in the form of wedges, while the intervening portions of the primary medullary rays show a corresponding broadening outwards. Further, each phloem-group is bounded towards the primary cortex by a group of primary bast-fibres; groups of bast-fibres occur likewise in the secondary bast, and usually cause a distinct, more rarely (in the Ureneae, according to Dumont) an indistinct, stratification of the bast; according to Dumont, the secondary groups of hard bast are scanty in *Gossypium* and its allies as well as in the Durioneae.

The mucilage-receptacles and the features presented by the crystals in the axis have already been discussed above in the section on the leaf-structure.

I may add two observations regarding the **root**-structure of the Malvaceae. The first of these refers to Lanessan's statement as to the appearance of concentric layers of cork around a vessel or a group of vessels in the wood of the root of *Althaea officinalis*. The second is that, according to Van Tieghem, the development

[1] According to K. Schumann, *Ochroma Lagopus*, Sw. possesses an unusually light wood, consisting almost entirely of wood-parenchyma and vessels.

of primary hard bast, which elsewhere is rare in the root, is of frequent occurrence in this Order and, it may be added, in the Sterculiaceae and Tiliaceae also.

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STERCULIACEAE.

1. Review of the Anatomical Features. In agreement with the close relationship of the Sterculiaceae with the Malvaceae, the same anatomical features are found here as in the latter Order, namely, stellate and tufted hairs, the same form and structure of the phloem in the vascular bundles of the stem, and lastly, mucilage-receptacles. The latter are either cells with mucilaginous membranes, (lysigenous) mucilage-cavities or (schizogenous or lysigenous ?) mucilage-canals. The mucilage-canals are especially characteristic of the Sterculieae and Dombeyeae, but belong also to genera of other tribes.

The leaves of most members of the Order are bifacial in structure; the stomatal apparatus belongs to no special type. The petiole as a rule contains medullary bundles in the middle of a bundle-ring. The cork arises in the outermost cell-layer of the primary cortex. The wood consists (*a*) of medullary rays of varied breadth, (*b*) of vessels which vary in their arrangement and size of lumen and usually have simple, very rarely (*Lasiopetalum*) few-barred perforations, (*c*) of wood-parenchyma developed in varying abundance, and (*d*) of wood-prosenchyma, which as a rule bears simple pits, but has typical bordered pits in the Lasiopetaleae.

Besides the stellate and tufted hairs already mentioned, the following structures also contribute to form the hairy covering: simple unicellular or uniseriate hairs, glandular and peltate hairs (Fig. 35). Oxalate of lime occurs in the form of clustered and of ordinary solitary crystals, rarely also of small prismatic crystals. Tannin is usually present in abundance.

The following specially noteworthy features have been demonstrated in the Order: hypoderm in the leaf (*Ungeria floribunda*); a xylem-mass with tier-like structure (*Pterospermum suberifolium*, Lam.); medullary, concentrically

constructed vascular bundles with centrally placed phloem (stem of *Leptonychia urophylla*).

2. Structure of the Leaf. On this subject the following facts may be pointed out, on the authority of Dumont[1]. The leaf-structure is mostly bifacial; rarely (*Reevesia*) the whole mesophyll consists of palisade-tissue. The **epidermal cells** sometimes (*Sterculia*) have a thick cuticle; in *Theobroma Cacao*, they are of considerable size on the upper side of the leaf. Gelatinization of the epidermis is common (e.g. in *Sterculia*). In *Ungeria floribunda*, a one-layered hypoderm containing clustered crystals has been observed. The **stomata** present the same features as in the Malvaceae; no specially pronounced type in the arrangement of the neighbouring cells occurs. Regarding the structure of the **petiole** Van Tieghem and Dumont point out that the ring of bundles in most members of the Order encloses an inner arc of wood and bast, which is open on the upper side; this is wanting in the Buettnerieae and Lasiopetaleae only. In *Sterculia acerifolia* and in *Theobroma Cacao*, Petit describes a bundle-ring as occurring in the characteristic region; in the initial region a ring likewise occurs in *Sterculia*, but in *Theobroma* there are four vascular bundles which are orientated in the form of an orthogonal cross.

As in the Malvaceae, **mucilage-receptacles** are also frequent in the Sterculiaceae. They are either cells with mucilaginous membranes, or lysigenous secretory cavities, derived from groups of similar cells, or lastly mucilage-canals, which, according to Van Tieghem, have a schizogenous, according to Dumont a lysigenous, origin.

The mucilage-canals are present in varying abundance in the individual species; they vary also with regard to their diameter. They are found in the pith and primary cortex of the branches, or in the pith only; further, they occur in the ground-tissue of the petiole, while they are absent in the root. In the pith they form one or two more or less regular circles, but in the primary cortex only one. The medullary mucilage-canals of the single circle or, when two of these are present, those of the outer circle, are situated either opposite the primary xylem-groups of the bundle-ring (*Dombeya*, *Heritiera*, *Tarrietia*, according to Van Tieghem), or alternating with them (*Eriolaena*, *Melhania*, *Sterculia*, according to Van Tieghem).

Regarding the distribution of the mucilage-canals within the Order the general statement may be made that, according to the existing investigations, these structures are characteristic of the tribes Sterculieae and Dombeyeae, and that in the other tribes of the Sterculiaceae they only occur sporadically.

Regarding the details of their distribution, we may give the following short statement of Dumont and Van Tieghem's results. Mucilage-canals are found:

(I.) in the pith and primary cortex of the branch, as well as in the parenchyma of the petiole in: *Sterculia Balanghas*, *S. diversifolia*, *S. mexicana*, *S. platanifolia*; *Brachychiton acerifolium*, *B. populneum*; *Tarrietia Argyrodendron*, *T. javanica*; *Cola acuminata*, *C. cordifolia*; *Eriolaena Wallichii* (but not in *E. Hookeriana*); *Pterospermum acerifolium*, *P. platanifolium*;

(II.) in the pith, but not in the cortex of the branch, besides being usually present in the parenchyma of the petiole in: *Heritiera macrophylla*, *Dombeya* '*libidiniflora*' (Dumont), *D. mollis*, *D. natalensis*, *Trochetia Boivini* (*sphalmate*

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[1] Dumont, Ann. sc. nat., 1887, loc. cit. The following genera, in the enumeration of which I follow the classification of Bentham and Hooker, were investigated by Dumont:

Tribe 1. Sterculieae: *Sterculia* (incl. *Brachychiton*), *Tarrietia*, *Cola*, *Heritiera*; tribe 2. Helictereae: *Reevesia*, *Ungeria*, *Kleinhovia*, *Helicteres*, *Pterospermum*; tribe 3. Eriolaeneae: *Eriolaena*; tribe 5. Dombeyeae: *Ruizia*, *Dombeya*, *Cheirolaena*, *Trochetia*, *Pentapetes*, *Melhania*; tribe 6. Hermannieae: *Hermannia*, *Mahernia*, *Melochia*, *Waltheria*; tribe 7. Buettnerieae: *Abroma*, *Theobroma*, *Guazuma*, *Leptonychia*, *Ayenia*, *Buettneria*, *Rulingia*, *Commersonia*; tribe 8. Lasiopetaleae: *Seringia*, *Kerandrenia*, *Thomasia*, *Guichenotia*, *Lasiopetalum*.

'*Boivira*' in Dumont's work), *Cheirolaena linearis, Ruizia lobata, Melhania ferruginea, M. Kotschyi, Pentapetes acerifolia, P. suberifolia, Theobroma Cacao, Abroma angusta, Guazuma ulmifolia, Seringia platyphylla.*

Regarding the distribution of the mucilage-cavities and mucilage-cells in the axis and in the leaf, I will only refer to the most important facts in broad outline, and for other particulars will refer to the more detailed statements of Dumont. These two kinds of mucilage-receptacle are to be met with in all the tribes, but not in all the genera and species; they occur in the bast and in the primary cortex of the branch, as well as in the ground-tissue of the petiole. They are, as Dumont mentions in summarizing the subject, fairly numerous in the cortex of the Dombeyeae, often absent in the branch and leaf of the Helictereae, numerous in the leaf, but scanty in the branch of the Buettnerieae and Hermannieae, and are developed in small numbers in all the tissues of the Lasiopetaleae.

Oxalate of lime, as a rule, takes the form of clustered or solitary crystals. K. Schumann's statement as to the occurrence of raphides in the Sterculiaceae is erroneous and is perhaps due to a misinterpretation of a citation made by Dumont, according to which small prismatic crystals are present in the mesophyll in *Leptonychia urophylla* and *Ayenia magna*. The clustered crystals of the leaf-tissue are sometimes large, and they then occupy enlarged cells of the palisade-tissue (*Rulingia pannosa*). We may here refer to the abundant tannin contained in the tissues of the Sterculiaceae.

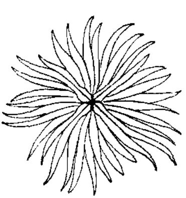

FIG. 35. Peltate hair of *Heritiera macrophylla*, Hort. Calcutt.—After O. Bachmann.

The **hairy covering**, like that of the Malvaceae, consists of simple unicellular or uniseriate hairs, of glandular hairs, similar in nature to those of the Malvaceae, of tufted or stellate hairs, which are sometimes seated on an emergence, and lastly of peltate hairs. Peltate hairs, according to O. Bachmann and Dumont, are present in *Heritiera Fomes*, Buch.-Ham., *H. littoralis*, Ait., *H. macrophylla*, Hort. Calcutt. (Fig. 35), *Tarrietia Argyrodendron, Trochetia uniflora*, DC., *T. Boivini, Dombeya* sp. Hildebr. No. 3575, and in *Cheirolaena linearis*. According to O. Bachmann, the peltate hairs are of varied structure. The peltate scales of species of *Heritiera* show a peculiar arrangement of their wide-lumened ray-cells in relation to two middle lines, which are at right-angles to one another; those of *Trochetia uniflora* have a small upper scale of half the diameter of the principal 'shield,' and those of *Dombeya* sp. present no special structure beyond having ray-cells with thick walls. According to Dumont, spiny emergences occur in *Eriolaena Hookeriana* and species of *Buettneria*.

3. STRUCTURE OF THE AXIS. An examination of the **wood** in twelve genera belonging to the different tribes[1] led to the following general results. The medullary rays of the wood vary in breadth; thus they attain a breadth of ten cells in *Sterculia coccinea*, Roxb., but are only one to two cells broad in *Hermannia chrysophylla*, Eckl. et Zeyh. Variation is likewise found in the arrangement of the vessels and in the size of their lumina (maximum diameter =·024 to ·1 mm.). In the majority of the species bordered pitting is present on

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[1] Solereder, Holzstruktur, 1885; species of the following genera were investigated: *Sterculia, Heritiera, Helicteres, Reevesia, Dombeya, Melhania, Hermannia, Waltheria, Buettneria, Commersonia, Lasiopetalum, Thomasia*; see also Möller, loc. cit., regarding *Dombeya, Guazuma*, and *Sterculia*.

the vessel-wall where it is in contact with ray-parenchyma; on the other hand, in *Sterculia coccinea*, transitions to simple pits are found on these parts of the wall. Spiral thickening of the walls of the vessels has been observed in *Reevesia Wallichii*, R. Br. and *Heritiera macrophylla*, Hort. Calcutt. The perforations of the vessels are simple; but accompanying this type scalariform perforations with 1–2 bars are met with in *Lasiopetalum Gunnii*, Steetz. According to the species the wood-parenchyma is developed in varying abundance. The wood of *Sterculia coccinea*, *Heritiera macrophylla* and *Reevesia Wallichii*, is very rich in wood-parenchyma. In the genera of the Lasiopetaleae (*Lasiopetalum* and *Thomasia*) the wood-prosenchyma is provided with bordered pits, elsewhere only with simple or with narrowly and indistinctly bordered pits. The wood-prosenchyma either has wide lumina and thin walls, or in some cases thick walls and narrow lumina, e.g. in *Hermannia chrysophylla*, Eckl. et Zeyh., and in the Lasiopetaleae. Xylem with tier-like construction of the medullary rays has been met with by Höhnel in *Pterospermum suberifolium*, Lam.

With regard to the structure of the **cortex** it may first be mentioned that the cork, as far as has been observed, always arises in the outermost cell-layer of the primary cortex. Sclerosed cells are stated by Dumont and Möller to occur in the cork of *Reevesia* and of *Sterculia cordifolia*, Cav. According to Dumont the cork of the Lasiopetaleae has a characteristic appearance in a transverse section of the branch, inasmuch as the radial walls of the rows of cork-cells form zigzag lines. Stone cells are met with in the middle of the primary cortex in some cases, e.g. in *Tarrietia Argyrodendron*, *Cola*, and *Ungeria*, according to Dumont. The bast has essentially the same form and structure as in the Malvaceae and Tiliaceae; the primary medullary rays of the bast are broadened outwards in the form of wedges, between the groups of bast, which consequently become narrower in the same direction; the secondary groups of hard bast are more or less distinctly arranged in tangential bands, and thus stratification of the bast of varying distinctness is produced.

The twining species, which are restricted to the genus *Buettneria*, are normal in structure. Medullary vascular bundles (with centrally placed phloem) have been observed (Dumont) in *Leptonychia urophylla* only.

Literature: Trécul, Mucilages, Adansonia, t. vii, 1866–7, p. 248 et seq.—Möller, Holzanat., Denkschr. Wien. Akad. 1876, pp. 78, 79 and 374.—Möller, Rindenanat., 1882, pp. 243–5.—Höhnel, Stockwerk. aufg. Holzk., Sitz.-Ber. Wiener Akad., Bd. lxxxix, Abt. 1, 1884, p. 42.—Klöppel, Sekretbeh., Diss., Halle a. S., 1885, see also Zeitschr. f. Naturw., Bd. lviii, pp. 159–96.—Solereder, Holzstr., 1885, pp. 84–6.—Van Tieghem, Can. à gomme des St., Bull. Soc. bot. de France 1885, p. 11 et seq. and Ann. sc. nat., sér. 7, t. i, 1885, pp. 75–9.—Bachmann, Schild., Flora 1886, separate copy, pp. 33, 34.—Plitt, Blattst., Diss., Marburg, 1886, p. 37.—Dumont, Ann. sc. nat., sér. 7, t. vi, 1887, p. 198 et seq. and pl. 7.—Petit, Pétiole, Mém. Soc. sc. phys. et nat., sér. 3. t. iii, 1887, pp. 302, 303.—Schumann, in Natürl. Pflanzenfam., 3. Teil, Abt. 6, 1890, pp. 69, 70.—Schenck, Anat. d. Lianen, 1893, pp. 77, 78.—Walliczek, Membranschl., Pringsheim Jahrb., Bd. xxv, 1883, pp. 254 et seq.—[Mangin, Gomme chez les St., Compt. rend., t. cxxv, 1897, pp. 725–8.]

TILIACEAE.

1. Review of the Anatomical Features. In their anatomical structure the Tiliaceae show their relation to the Sterculiaceae and Malvaceae. In the Holopetalae (of Bentham and Hooker), with the exception of *Muntingia*, mucilage is found in cells or in cavities, the latter when situated in the pith being sometimes elongated like canals (e.g. in *Luhea*, *Corchorus*, &c.), while in the Heteropetalae and in *Muntingia* it is usually absent; in the Heteropetalae, however, mucilaginous cells sometimes occur in the epidermis of the leaf.

The stomata have no special subsidiary cells. The veins are embedded in the mesophyll; more rarely (Brownlowieae) they are vertically transcurrent by means of sclerenchyma. Oxalate of lime occurs in the form of ordinary clustered or solitary crystals, in *Tilia* and in *Solmsia* also in the form of styloid-like crystals. Resin-cells have been observed in *Hasseltia* and *Prockia*, caoutchouc-receptacles resembling laticiferous tubes in *Plagiopteron*. The hairy covering consists of simple unicellular or uniseriate hairs, as well as tufted, peltate and glandular hairs.

The wood contains (*a*) vessels with simple perforations, but occasionally with scalariform perforations side by side with the former, and (*b*) wood-prosenchyma with simple pits, and usually possessing relatively wide lumina. The vessel-walls, where they are in contact with parenchyma of the medullary rays, possess simple pits or bordered pits which sometimes pass over into simple pits. The varying breadth of the medullary rays, the varying diameter and arrangement of the vessels, the occurrence or absence of spiral thickening on the walls of the vessels, the varied nature of the wood-prosenchyma, which is sometimes septate by means of a few division-walls, and the varying abundance of wood-parenchyma can all be made use of for specific diagnosis, and probably in part for generic diagnosis also.

The nature of the bast is as a rule the same as in the Sterculiaceae and Malvaceae. The bast-portions of the vascular bundles are narrowed outwards in the form of wedges; between them the primary medullary rays become broader in the same direction. The primary hard bast, in this case, consists of isolated bands, which are separated by the tissue of the primary medullary rays, while in *Elaeocarpus*, *Prockia*, and *Hasseltia*, the outer limit of the bast is formed by an interrupted and composite sclerenchymatous ring. In most members of the Order the secondary bast is characterized by the possession of hard bast, which is generally developed in layers. Secondary hard bast is wanting in *Prockia* and *Hasseltia* only. The cork arises immediately beneath the epidermis.

2. STRUCTURE OF THE LEAF. According to the statements of Dumont[1] the **mesophyll** is bifacial in structure in the majority of the species. In the Brownlowieae investigated (species of the genera *Berrya*, *Diplodiscus*, &c.) as well as in *Muntingia* and *Apeiba*, the whole of the mesophyll consists of palisade-cells. Mucilaginous **epidermal cells** are described by Dumont in *Glyphaea grewioides* and *Desplatzia subericarpa*, by Van Tieghem in *Solmsia*[2], and by Szyszylowicz in certain Elaeocarpeae and Sloaneae. In the two tribes last named the epidermis is occasionally many-layered, according to Szyszylowicz. I have observed a one-layered hypoderm on the upper side of the leaf in *Plagiopteron fragrans*, Griff.; this tissue in places contains clustered crystals, which also occur in considerable numbers in the lower epidermis. In the Tiliaceae the **stomata** are not accompanied by any special subsidiary cells, and are generally present only on the lower surface of the leaf; in *Aristotelia* water-pores occur, according to Reinke. In the Brownlowieae the **veins** are vertically transcurrent both above and below by means of sclerenchyma; in the other tribes the vascular bundles of the veins are embedded in the mesophyll.

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[1] Dumont's (1887) investigations extend to the following genera: tribe 1. Brownlowieae: *Brownlowia*, *Pentace*, *Diplodiscus*, *Pityranthe*, *Christiania*, *Berrya*, *Carpodiptera*; tribe 2. Grewieae: *Grewia*, *Desplatzia*, *Duboscia*, *Erinocarpus*, *Vasivaea*, *Triumfetta*; tribe 3. Tilieae: *Entelea*, *Sparmannia*, *Corchorus*, *Luhea*, *Mollia*, *Muntingia*, *Tilia*; tribe 4. Apeibeae: *Glyphaea*, *Apeiba*; tribe 5. Prockieae: *Prockia*, *Hasseltia*; tribe 7. Elaeocarpeae: *Elaeocarpus*, *Aristotelia*.

[2] The genus *Solmsia*, newly founded by Baillon, and at first included by him in the Tiliaceae, but subsequently (Bull. Soc. Linn., 1888, p. 728) in the Thymelaeaceae, is one of the Tiliaceae on the evidence of its anatomical features; according to Van Tieghem it possesses mucilaginous epidermal cells, prismatic crystals, bast like that of the lime and (this being the decisive point) simply collateral vascular bundles.

Oxalate of lime is usually deposited in the form of ordinary solitary or clustered crystals. In *Tilia* (bast of the axis) and in *Solmsia* prismatic crystals of oxalate of lime, resembling styloids in form, occur.

As in the nearly allied Orders Sterculiaceae and Malvaceae, some of the Tiliaceae are characterized by **mucilage-contents**, which occur both in the axis and in the leaf. Szyszylowicz's researches on the structure of the axis have shown that the Tiliaceae may be divided into two groups in relation to their mucilage-contents; the first of these comprises the genera which are characterized by the presence of mucilage-cells, or of lysigenous mucilage-spaces, both in the cortex and in the pith, or only in one of these tissues; to this group belong all the genera included in the Holopetalae of Bentham and Hooker (Brownlowieae, Grewieae, Tilieae, and Apeibeae) with the exception of *Muntingia*. The second group includes the genera without mucilage-contents; viz. all the Acropetalae of Bentham and Hooker (Prockieae, Sloaneae, Elaeocarpeae), as well as *Muntingia*. The more detailed statements of Dumont, as to the occurrence and absence of mucilage-receptacles in the genera investigated by him, coincide with these results of Szyszylowicz.

The following statements may be extracted from Dumont's detailed observations on this subject. The Brownlowieae investigated contain mucilage in numerous cells or cavities; mucilage is entirely wanting in only one species, namely, *Pityranthe verrucosa*. Among the Tilieae, *Tilia* possesses mucilage-cells and mucilage-cavities, neither being specially numerous; *Muntingia* is characterized by the absence of mucilage; in *Luhea, Corchorus, Mollia, Entelea*, and *Sparmannia* (which, according to Bentham and Hooker, likewise belong to the tribe Tilieae, but are included by Dumont in the Grewieae) greatly elongated mucilage-cavities, differentiated like canals, are found in the pith. Among the Grewieae this type of mucilage-cavity also occurs in the genera *Vasivaea* and *Erinocarpus*, while in *Grewia, Desplatzia, Triumfetta*, and *Duboscia*, belonging to the same tribe, they are replaced by mucilage-cavities, which are only slightly elongated. Among the Apeibeae, *Apeiba* shows the same features as *Luhea, Vasivaea*, &c., i.e. it possesses elongated mucilage-spaces in the pith, while only mucilage-cells have been observed in *Glyphaea*.

In connexion with the mucilage-receptacles we may mention Szyszylowicz's statement as to the occurrence of **secretory cells** with yellow contents, resembling gum-resin, in the bast of *Hasseltia* (abundant) and *Prockia* (scanty), and of Radlkofer's observation regarding the occurrence of elements filled with caoutchouc in the cortex and medullary sheath and in the leaf-tissue of the monotypic genus *Plagiopteron*. The latter secretory organs are elements resembling laticiferous tubes; in the leaf they are restricted to the veins, where they are found in abundance below the bast-portion of the vascular bundles. On breaking the leaf they become visible to the naked eye as elastic threads.

The **hairy covering** consists of unicellular or uniseriate (*Triumfetta pilosa*) simple hairs, of stellate and tufted hairs, the rays of which are usually unicellular, though sometimes uniseriate (Grewieae), of peltate hairs, and of glandular hairs. The uniseriate hairs of *Triumfetta pilosa* referred to above are embedded in emergences. According to O. Bachmann the peltate hairs have no specially characteristic form; their ray-cells are numerous and have fairly thick walls, and each of them runs out into a point. Small scales of this kind are stated to occur in species of *Brownlowia, Pentace, Mollia*, and also in *Diplodiscus*. In *Triumfetta heterophylla*, Lam., I have met with stalked glandular hairs, having a multicellular head, and unicellular glandular hairs, consisting of pear-shaped epidermal cells. With these structures we may class the colleters, which were found by Reinke on the leaf-teeth of *Aristotelia Macqui*; they occur above the terminations of the veins, and consist of a nucleus of elongated parenchymatous cells and of a palisade-like secretory epidermis, the cells of which are elongated at right angles to the central cells.

In the characteristic region of the **petiole** in most of the species investigated a closed ring of wood and bast is found, and sometimes internal to this one or more medullary bundles. In *Aristotelia Macqui*, L'Hérit., the main system is not closed, but consists of three parts, a large arc-shaped bundle below, and two smaller upper strands, which together form a circle; besides these, there is one vascular bundle corresponding to the angle of the petiole on each side of the groove.

3. Structure of the Axis. Regarding the structure of the **wood** the following points may be referred to in accordance with my earlier statements[1]. The breadth of the medullary rays varies considerably within the Order; they are often broad, but sometimes not more than three cells in breadth, e. g. in *Elaeocarpus robustus*, Roxb. Nor do the arrangement of the vessels and the size of their lumina (maximum diameter between ·03 and ·12 mm.) afford any features constant for the whole Order. According to Dumont, in most members of the Order with the exception of the genera of the tribe Tilieae, the vessels form long radial rows in a transverse section of the branch. Where the vessel-walls touch the medullary rays, we find either simple (*Elaeocarpus*, *Sloanea*, *Echinocarpus*), or more frequently one-sided bordered pits, often with transitions to simple pits (e. g. in *Pentace* and *Sparmannia*). Spiral thickening of the vessel-wall has been observed in *Tilia parvifolia*, Ehrh. and *Echinocarpus assamicus*, Benth. Differences are also found in the Order with regard to the perforations of the vessels. In the representatives of the tribes Prockieae, Sloaneae, and Elaeocarpeae hitherto investigated, a tendency to the formation of scalariform perforations in the vessels is recognizable; simple, much-elongated, elliptical perforations occur in *Elaeocarpus robustus*; accompanying these latter in *Prockia* and the Sloaneae which have been investigated scalariform perforations occur. Besides the above-mentioned types, simple perforations of the ordinary circular or elliptical form are found. The wood-parenchyma varies greatly in abundance; in *Brownlowia elata*, Roxb. and in *Pentace triptera*, Mast., it plays a very prominent part in the formation of the wood. The wood-prosenchyma has simple pits on its walls, but sometimes a more or less distinct narrow border is present; for the most part the wood-prosenchyma has relatively wide lumina, and only rarely (*Pentace*) thick walls and narrow lumina. Thin division-walls have been observed in the wood-prosenchyma of *Echinocarpus assamicus*, Benth., *Elaeocarpus robustus*, Roxb., *Prockia Crucis*, L., and *Sloanea australis*, F. v. Müll.

The following facts relating to the structure of the **cortex** are known from the investigations of Möller and Dumont. The cork arises in the outermost cell-layer of the primary cortex. In *Tilia* the walls of the cork-cells are fairly thin and the lumina are strongly compressed in the radial direction. According to Dumont, sclerotic cork-cells occur in the Brownlowieae, in *Vasivaea* and *Apeiba*; cork-cells, thickened on one side (on the inner tangential wall) in *Luhea grandiflora*, Mart., according to Möller. In the Tiliaceae—with the exception of the Prockieae—three zones may be distinguished in the primary cortex, according to Dumont, viz. an outermost parenchymatous, a middle collenchymatous, and an inner parenchymatous zone. In a transverse section the bast-portions of the vascular bundles show the form of a trapezium narrowed outwards, while the intervening primary medullary rays consequently become broader outwards. The groups of bast are bounded towards the primary cortex by bands of primary bast-fibres. An exception in this respect is formed by the genera *Elaeocarpus*, *Prockia*, and *Hasseltia*, in which the

[1] Species of the genera *Brownlowia*, *Pentace*, *Grewia*, *Columbia*, *Sparmannia*, *Tilia*, *Apeiba*, *Prockia*, *Sloanea*, *Echinocarpus* and *Elaeocarpus* were investigated by me; species of *Luhea* and *Muntingia* by Möller.

pericycle is formed by a more or less interrupted sclerenchymatous ring, composed of small groups of primary bast-fibres and of stone-cells. In most cases the secondary bast is stratified owing to the presence of bands of hard bast; but sometimes the secondary hard bast is irregularly arranged, or (e.g. in *Elaeocarpus*) only represented by small strands; in *Prockia* and *Hasseltia* secondary hard bast is completely absent. Lastly, the hard bast-fibres do not always have thick walls and narrow lumina, as in *Tilia*, but occasionally (e.g. in the Grewieae and in certain Tilieae) have thin walls and relatively wide lumina.

Literature: Trécul, Mucilages, Adansonia, t. vii, 1866-7, p. 248 et seq.—Reinke, Sekretionsorg., Pringsheim Jahrb., Bd. x, 1876, p. 141.—Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 79, 80, and 375.—Areschoug, Blad. anat., Minesskrift, Lund, 1878, p. 51 et seq.—Möller, Rindenanat., 1882, pp. 245-8.—C. de Candolle, Anat. comp. d. feuilles, Mém. Soc. phys. et hist. nat., t. xxvi, 2, 1879, pp. 441, 442.—Solereder, Holzstr., 1885, pp. 86, 87.—Szyszylowicz, Syst. d. T., Engler, Bot. Jahrb., Bd. vi, 1885, p. 427 et seq. and Bd. vii, 1885, p. 133 et seq.—Bachmann, Schildh., Flora 1886, separate copy, p. 34.—Plitt, Blattstiel, Diss., Marburg, 1886, pp. 37, 38.—Dumont, Ann. sc nat., sér. 7, t. vi, 1887, pp. 179 and 225 et seq. and pl. 6, 7.—Petit, Pétiole, Mém. Soc. sc. phys. et nat. de Bordeaux, sér. 3, t. iii, 1887, pp. 303-7 and pl. iv.—Schumann, in Natürl. Pflanzenfam., 3. Teil, Abt. 6, 1890, pp. 1 and 9.—J. E. Weiss, Denkschr. Regensburg. bot. Gesellsch. 1890, separate copy, p. 66.—Strasburger, Bau u. Verr., 1891, pp. 219-33.—Radlkofer, Bot Gazette 1893, p. 199.—Van Tieghem, *Solmsia*, Ann. sc. nat., sér. 7, t. xvii, 1893, pp. 260, 261.—Walliczek, Pringsheim Jahrb., Bd. xxv, 1893, p. 209 et seq.—Wittlin, Kalkoxalattaschen, Bot. Centralbl. 1896, iii, p. 67.—Kuhla, Phelloderm, Bot. Centralbl. 1897, iii, p. 225.—Reiche, Chilen. Holzgew., Pringsheim Jahrb., Bd. xxx, 1897, p. 87.

LINEAE.

1. Review of the Anatomical Features. Among the few facts known concerning the anatomy of this Order it may be pointed out that the stomatal apparatus belongs to the Rubiaceous type, that oxalate of lime is met with only in the form of ordinary solitary crystals, that the hairy covering is constituted by unicellular simple trichomes and by glandular shaggy hairs; further, that the perforations of the vessels are mostly simple, being rarely accompanied by others of the scalariform type, and lastly, that the wood-prosenchyma usually bears bordered, more rarely (*Reinwardtia*) simple pits.

Special features to be mentioned here are: mucilaginous epidermal cells in the leaf (*Hugonia*, *Linum*), peculiar spiral tracheides in the mesophyll (*Ochthocosmos Roraimae*, Benth.), formation of papillae on the lower epidermis of the leaf (*Erythroxylon Coca*, Lam.).

2. Structure of the Leaf. The following statements are chiefly based on my own general preliminary investigation of some few species[1]. The leaf-structure in these is bifacial. The **epidermal cells** have straight to undulated lateral walls. Mucilaginous epidermal cells are stated by Radlkofer to occur in species of *Hugonia*, where they cause transparent dots, and by Wagner in *Linum catharticum*. In all investigated species the stomata are accompanied by subsidiary cells, which are directed parallel to the pore. The stomata occur either on both sides of the leaf (*Linum viscosum*) or only on the lower side (the remaining species cited). The smaller vascular bundles of the **veins** are embedded in the mesophyll, and are either accompanied by abundant sclerenchyma, (e.g. in *Hugonia Jenkinsii*), or by a small amount (in *Erythroxylon Coca*), while sclerenchyma is wanting in *Linum viscosum*. The spiral tracheae, which run free in the mesophyll in *Ochthocosmos Roraimae*, and are similar to the well-known spiral cells of *Nepenthes*, form a special feature.

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[1] Namely: *Linum viscosum*, L., *Hugonia Jenkinsii*, F. v. Müll., *Erythroxylon Coca*, Lam., *Ochthocosmos Roraimae*, Benth., *Ixonanthes icosandra*, Jack.

Oxalate of lime has hitherto only been observed in the form of solitary crystals. In *Linum austriacum* Zimmermann met with fairly large acicular crystalloids in the nuclei of the epidermal cells. Regarding the **hairy covering** it may be mentioned that in *Linum viscosum* long narrow unicellular trichomes occur, and that on the leaf-margin of the same plant there are glandular shaggy hairs with a long multiseriate stalk and spherical head, the epidermal cells of which are elongated like palisade-cells in the radial direction.

3. STRUCTURE OF THE AXIS. The structure of the **wood** has been investigated in species of *Reinwardtia, Hugonia, Roucheria, Hebepetalum,* and *Ixonanthes*. The medullary rays are 1–2-seriate (*Erythroxylon*) or as much as 4-seriate (*Hugonia*). The vessels attain a diameter of ·07 mm. In *Hugonia* and *Roucheria* their walls bear bordered pits where they are in contact with parenchyma of the medullary rays; in the remaining genera the walls have transitions from bordered to large simple pits at these places. In *Roucheria Griffithiana*, Planch., delicate spiral thickening of the pitted vessels has been observed. The perforations of the vessels are for the most part exclusively simple and circular or elliptical; in *Ixonanthes icosandra* they are in part scalariform with few or many bars. The development of the wood-parenchyma varies. In *Hugonia Mystax*, L., and in *Roucheria Griffithiana* it is restricted to the neighbourhood of the vessels; in *Erythroxylon Coca* and *Hebepetalum latifolium*, Benth. it is fairly abundant, and in *Ixonanthes icosandra* it forms tangential bands in the xylem. In *Hugonia, Roucheria,* and *Ixonanthes*, the wood-prosenchyma bears typical bordered pits on its walls; in *Erythroxylon* there are small but for the most part distinct bordered pits; in *Reinwardtia*, where the wood-prosenchyma is locally provided with a slight gelatinous layer (' Gallertschicht ') and with delicate cross-walls, it bears simple pits.

The structure of the **cortex** has so far been very little investigated. It can only be stated that the species of *Linum* are characterized by long [1] (according to Kallen, multinucleate) bast-fibres, and further, that the cortical structure of *Erythroxylon Coca* is known from Möller's work. In this species the cork consists of small cells with wide lumina, and arises subepidermally. The primary bast-fibres form an interrupted ring, which is often only uniseriate, and the interspaces do not become sclerosed. The secondary bast consists of soft bast only.

Literature: Möller, Denkschr. Wiener Akad. 1876, pp. 90 and 386.—Kallen, Flora 1882, p. 92.—Möller, Rindenanat., 1882, p. 273.—Solereder, Holzstr., 1885, pp. 87, 88.—Radlkofer, Sitz.-Ber. Münch. Akad. 1886, p. 304.—Tschirch, Ang. Pfl.-Anat., 1889, pp. 323 and 438.—Reiche, in Natürl. Pflanzenfam., 3. Teil, Abt. 4, 1890, pp. 28, 38, and 40. — Zimmermann, Pflanzenzelle, 2. Heft, 1891, p. 126.—A. Wagner, Sitz.-Ber. Wiener Akad., Bd. ci, Abt. 1, 1892, p. 515.—Herbst, Bot. Centralbl. 1894, i, p. 327.

HUMIRIACEAE.

This small Order, which consists almost solely of American species, shows for the most part uniform features as regards the structure of the wood [2]. The medullary rays are 1–2-seriate; the vessels (maximum diameter = ·072 mm.) are mostly isolated. The perforations of the vessels are scalariform throughout

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[1] Length = ·2 – 1·4 mm. according to Wiesner.

[2] Solereder, Holzstruktur, 1885, p. 88: species of the three genera *Vantanea, Humiria,* and *Sacoglottis* have been investigated; the plant named *Helleria oblongifolia*, Mart. MSS. in my ' Holzstruktur ' is only a form of *H. obovata*, Nees et Mart. (= *Vantanea obovata*, Benth.). See also: Möller, Holzanat., Denkschr. Wiener Akademie, 1876, pp. 83 and 379; Hanausek and Kutscher, Humiriholz, Zeitschr. allg. österr. Apoth.-Ver., 1886, pp. 408–11 and 3 Figs.; Reiche, Natürl. Pflanzenfam., 3. Teil, Abt. 4, 1890, p. 35.

and have many bars. The wood-parenchyma is developed in abundance. The pitting on the walls of the vessels, where they are in contact with parenchyma of the medullary rays, likewise varies; in the same position *Humiria* and *Sacoglottis* have bordered pits, which are sometimes arranged in a scalariform manner, while *Vantanea* has simple pits with transitions to bordered pits. In all three genera the wood-prosenchyma bears bordered pits.

The three species investigated with respect to their **cortical structure** (*Vantanea obovata*, Benth., *Humiria floribunda*, Mart., *Sacoglottis amazonica*, Mart.) agree primarily in the possession of a composite and continuous sclerenchymatous ring in the pericycle. Development of cork takes place subepidermally in *Humiria* and *Sacoglottis*. The cork usually consists of thin-walled cork-cells, somewhat compressed in the radial direction, and in *Vantanea obovata* it includes cells which are strongly thickened on their inner tangential walls. In the species of *Humiria* and *Sacoglottis* mentioned, the primary cortex contains stone-cells; in the same species the secondary bast includes groups of secondary bast-fibres, between which the tissue of the medullary rays sometimes becomes sclerosed. Oxalate of lime is excreted in the neighbourhood of the sclerenchyma in the form of ordinary solitary crystals, in the soft bast in the form of clustered crystals.

There is nothing particular to remark regarding the structure of the **leaf**, which I have investigated in *Vantanea obovata*, Benth., *Humiria crassifolia*, Mart., and *Sacoglottis amazonica*, Mart. The leaves are leathery and bifacial in structure. In *Humiria* and *Sacoglottis* each stoma is surrounded by several neighbouring cells; in *Vantanea obovata* subsidiary cells adjoin the guard-cells; they are arranged parallel to the pore, and are usually divided by a wall perpendicular to the latter. In *Humiria crassifolia* clustered crystals have been observed in the mesophyll; in *Sacoglottis amazonica*, solitary crystals which are not well differentiated.

A **hairy covering** is rare in this Order. The trichomes in the floral region of *Vantanea obovata* are simple unicellular or uniseriate hairs. Special internal secretory receptacles, the occurrence of which one might be led to expect from Bentham and Hooker's statement 'arbores vel arbusculae balsamifluae' (see also Flora brasil., vol. xii, 2, pp. 453, 454), are wanting in the Humiriaceae. The glandular dots on the margin of the leaf of *Humiria*, which are mentioned by Bentham and Hooker, and (e.g. in *H. floribunda*, Mart. var. *ε laurina*, Urb.) can be seen even by the naked eye, are rather large external glands[1], which are not differentiated in the form of hairs. They have a secretory epidermis, which is differentiated like palisade-tissue, and is seen in surface-view to consist of small cells with thin walls.

MALPIGHIACEAE.

1. Review of the Anatomical Features. This Order is distinguished by the following anatomical characters: (*a*) the occurrence of unicellular one- or two-armed trichomes (Fig. 36), which are replaced by unicellular hairs of star-like form (Fig. 36, G) in *Thryallis* only; (*b*) the absence both of ordinary glandular hairs and of internal secretory organs; (*c*) the type of stoma with subsidiary cells arranged parallel to the pore; (*d*) the simple perforations of the vessels; and (*e*) the simple pitting of the wood-prosenchyma,

[1] In *Vantanea*, e.g. *V. obovata*, similar external glands occur also on the outer side of the sepals.

which is sometimes septate. For the recognition of sterile material the large glands, which are met with on the margin, or on the lower side of the leaf, or on the petiole, are also of value; they are visible even to the naked eye, and have a complicated structure. Oxalate of lime is usually excreted in the form of clustered and solitary crystals, rarely (*Peixotoa*) as styloids.

Special anatomical features in the structure of the leaf, occurring in certain species only, are: the occurrence of a many-layered epidermis, of mucilaginous epidermal cells and of fibre-like spicular cells in the mesophyll. Anomalous structure of the axis also occurs in the Order. Interxylary phloem is found in the genus *Dicella* and in *Stigmaphyllon jatrophaefolium*. Stems with a furrowed xylem-mass (Fig. 37, *A*) occur in species of *Tetrapteris*, *Heteropteris*, and *Peixotoa*; stems showing the same character together with subsequent cleavage of the xylem are found in species of *Tetrapteris* (Fig. 37, *B*), *Mascagnia*, *Mezia*, and *Banisteria*; stems with a normal outer cambium and with secondary cambium-formation in the wood-parenchyma, previously increased by dilatation, so that a splitting up of the whole mass of the stem is brought about, occur in *Stigmaphyllon*.

2. Structure of the Leaf. The following description is founded entirely on Niedenzu's statements in his revision of the Order for the 'Natürliche Pflanzenfamilien.'

The **leaf-tissue** is either centric or bifacial in structure. In most cases the assimilatory tissue consists of one layer (in species of *Byrsonima* and in a few other cases of 2–5 layers) of palisade-cells which are usually slender, and of 2–12 layers of spongy parenchyma, the lowest layer of which (more rarely the lowest two layers) become more or less palisade-like in many species of *Hiraea*, *Tetrapteris*, *Dinemagonum*, *Banisteria*, *Stigmaphyllon*, *Byrsonima*, &c.; rarely (*Stigmaphyllon dichotomum*, Griseb., *Byrsonima lucida*, DC., *B. coccolobaefolia*, H. B. K., &c.), the whole of the mesophyll consists of palisade-parenchyma; in *Tricomaria Usillo*, Hook. et Arn., palisade-tissue is present on both sides, spongy parenchyma in the middle. In *Stigmaphyllon angulosum*, Juss., and in several species of *Tetrapteris*, 1 or 2 layers of cells with very wide lumina and lying at the boundary between palisade and spongy parenchyma are differentiated into a kind of internal aqueous tissue. The longitudinal walls of the palisade-cells themselves also frequently become crumpled into transverse folds after the manner of aqueous tissue. The cells of the upper **epidermis** possess small lumina in species of *Hiraea* and in a few species of *Tetrapteris*, these being almost the only cases; in *Banisteria Clausseniana*, Juss., *Burdachia prismatocarpa*, Mart., *Byrsonima ferruginea*, H. B. K., *B. crassifolia*, H. B. K., &c., they have narrow lumina, but at the same time are as long as, or even longer, than the palisade-cells. In most cases they are fairly large, sometimes of unusual size; thus in *Camarea affinis*, St. Hil., *C. hirsuta*, St. Hil., *Gaudichaudia albida*, Cham. et Schlecht., this single layer exceeds the whole assimilatory system in thickness, the latter, it is true, being only 3–4 layers thick; in *Camarea affinis* the same holds good for the lower epidermis, which elsewhere exhibits large cells in a few species only. In most cases the lumina of the epidermal cells are of equal size; but in *Malpighia*, *Sphedamnocarpus*, *Ryssopteris* and other genera, extraordinarily large cells are found scattered among very much smaller elements; in *Banisteria parviflora*, Juss., and *Pterandra pyroidea*, Juss., these local water-reservoirs lie along the track of the veins in the upper and lower epidermis. The lower epidermis always, the upper epidermis for the most part, consists of one layer; in *Hiraea ternifolia*, Juss., it is locally two layers thick, owing to which—as in the case of epidermal cells with alternately large and small lumina—a dovetailing of epidermis and palisade-tissue is produced; in *Tetrapteris Guilleminiana*, Juss., &c., the upper epidermis becomes locally two-layered by division; in *Banisteria Mar-*

tiniana, Juss., and *Blepharandra hypoleuca*, Griseb., it is two-layered throughout, in *Tetrapteris rotundifolia*, Juss., two- or three-layered. Gelatinization of the epidermis is described by Radlkofer in *Triaspis squarrosa*, Radlk. In *Heteropteris oleaefolia*, Griseb., *Stigmaphyllon Sagraeanum*, Juss., *S. Lalandianum*, Juss., *Burdachia prismatocarpa*, Mart., &c., the epidermis on the lower side of the leaf is papillose. Stomata are almost always restricted to the lower side; in *Triaspis squarrosa* and *T. hypericoides* stomata are found on both sides of the leaf. The stomata have two subsidiary cells parallel to the pore; the pair of guard-cells is usually narrow and elongated-elliptical in surface-view; in several species of *Heteropteris* the pair is very small, circular, and deeply sunk; in *Byrsonima* on the contrary it is very large, circular, and provided with well-developed concentric ridges. The vascular bundles of the **veins** very frequently consist almost entirely of conducting elements. In most species of *Banisteria*, and specially of *Heteropteris*, hard bast and libriform are abundantly developed, although scarcely thick-walled. In *Tetrapteris fimbripetala*, Juss., *Stigmaphyllon Sagraeanum*, Juss., and *S. Lalandianum*, Juss., the vascular bundles of the veins give off sclerenchyma-fibres towards the epidermis on both sides. In *Heteropteris* especially a bundle consisting solely or almost solely of stereom runs along the leaf-margin near to or immediately below the epidermis, and consequently forms a kind of marginal bast.

Oxalate of lime is contained in the interior of the leaf and axis in the form of clustered or ordinary solitary crystals, which are unusually large in *Hiraea* and in certain species of *Banisteria*, &c.; all the species of *Peixotoa* are characterized by the fact that their assimilatory tissue, and especially the palisade-tissue, contains crystals resembling styloids, some of which are bent.

The **hairy covering** (Fig. 36) is formed of unicellular, two-armed [1], or star-shaped hairs. Niedenzu makes the following statements as to the detailed structure of these hairs. The two-armed hairs exhibit segmentation into a stalk (which may be short or very long, and stands up perpendicularly to the epidermis) and an upper portion; the latter is sometimes verrucose on the outer side, and may either be straight and boat-shaped, inserted at its centre at right angles to the stalk, and placed parallel to the epidermis, or may consist of two obliquely divergent branches, which are of equal or unequal length, and are straight or twisted in a serpentine manner. In the first case, the boat-like parts overlap one another like the tiles of a roof, and, when densely packed, give a golden or silvery metallic or silky sheen to the leaf-surface; in the latter case, the organ appears coated with a felt of varying compactness. The stinging hairs of the species of *Malpighia* and the bristle-hairs of the species of *Camarea* are similar unicellular two-armed hairs; but in the hairs of the genus *Camarea* (Fig. 36, *E*) one of the arms is reduced to a minimum. All the species of *Thryallis* are distinguished from the remaining members of the Order by the possession of star-shaped hairs (Fig. 36, *G*), i.e. trichomes, with a base of ob-conical form, from which several (as many as eight) arms radiate as in a star or sea-anemone. The stalks of the hairs are either sunk more or less deeply in the epidermis or they rest on short, few-celled pedestals. The walls of the hairs are either thin (e.g. in the malpighian hairs on the lower side of the leaf in *Peixotoa cordistipula*, Juss.) or thick and sclerotic (e.g. in the forked hairs of the upper side of the leaf in the same species).

A further characteristic of the Order is afforded by the well known large glands, which are not uncommonly met with on the petiole, on the lower side or on the margin of the leaf, and are also found on the calyx. According to

[1] Two-armed hairs have long been known in this Order and are familiar under the name of Malpighian hairs.

Martinet and Niedenzu they consist of a stratum of cells, frequently many-layered in the middle, the cells being more or less elongated at right angles to the surface of the gland; the outermost, secretory layer especially is differentiated like palisade-tissue (cf. Fig. 36, *H*).

3. Structure of the Axis. Regarding the structure of the wood, the following statements may be made in accordance with my general preliminary investigations, which extended to the genera *Malpighia, Burdachia, Banisteria, Peixotoa, Tetrapteris, Hiraea, Gaudichaudia,* and *Schwannia*. The diameter of the vessels is sometimes small (maximum = ·036 mm. in *Malpighia coccigera*, L.), in the twining species very large (maximum, e.g. = ·11 mm. in *Schwannia*

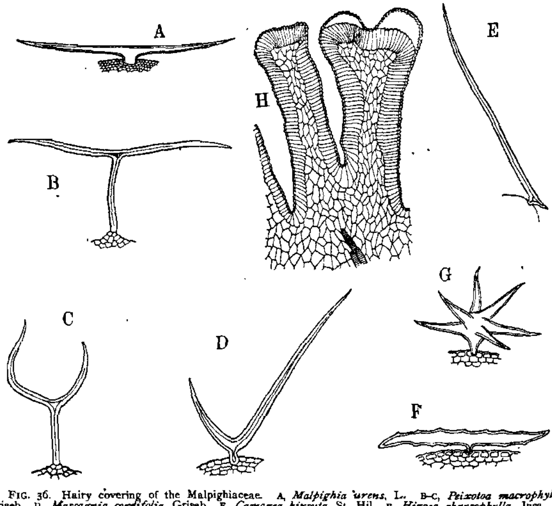

Fig. 36. Hairy covering of the Malpighiaceae. A, *Malpighia urens*, L. B–C, *Peixotoa macrophylla*, Griseb. D, *Mascagnia cordifolia*, Griseb. E, *Camarea hirsuta*, St. Hil. F, *Hiraea chrysophylla*, Juss. G, *Thryallis brachystachys*, Lindl. H, A piece of the margin of a calyx-gland of *Lophopterys splendens*, Juss.—After Niedenzu.

elegans, Juss.). The arrangement of the vessels varies. The medullary rays are usually only 1–3 rows of cells in breadth. The perforations of the vessels are simple and circular, or elliptical. On the portions of the vessel-wall in contact with the medullary rays bordered pits are usually found, in *Burdachia prismatocarpa*, simple pits as well. Spiral thickening of the walls of the vessels has been observed in *Peixotoa hispidula*, Juss. Wood-parenchyma is developed in varied abundance. It is usually restricted to the neighbourhood of the vessels but is more strongly developed in *Malpighia coccigera*, L., and in great abundance in *Burdachia prismatocarpa*; it contains solitary crystals in *Banisteria grata*, Griseb. and *Hiraea chrysophylla*, Juss. The wood-prosenchyma bears simple pits; septation of the elements occurs in *Tetrapteris inaequalis*,

Cav. and in *Hiraea chrysophylla* and, according to Möller, in an undetermined species of *Malpighia*. Unlignified parenchyma sometimes also takes part in the formation of the xylem-mass, e.g. according to Plitt, in *Heteropteris parvifolia*, DC. (erroneously described by him as '*parviflora*') and in the genus *Stigmaphyllon*, which is characterized by an anomalous xylem-mass (see below).

The structure of the **cortex** in this Order has been insufficiently investigated. Möller's statements are merely based on an examination of *Malpighia punicifolia*, L. and *Byrsonima spicata*, DC. In these species the periderm arises early and superficially and consists of cubical (*Malpighia*) or flat (*Byrsonima*) cells, certain layers being sclerosed on their inner tangential walls. The primary cortex contains groups of stone-cells and solitary crystals, in *Malpighia punicifolia* clustered crystals as well. A closed sclerenchyma-ring is not present on the outer side of the bast. The hard bast consists of unusually thick, delicately stratified and abundantly pitted bast-fibres, which are disposed in layers in the secondary cortex. The sieve-plates are simple and horizontal. The medullary rays of the bast have cells with wide lumina, sometimes in five series and in places are irregularly broadened. According to Vesque, in some cases e.g. in *Hiraea Houlletiana*, double-chambered crystal-fibres with clustered crystals occur in the bast. These arise by the fibrous cells first becoming septate by means of cross-walls, and by each of the chambers thus produced dividing by means of a longitudinal wall into two cells.

A number of species are characterized by **anomalous stem-structure.** Interxylary phloem is present in all the species of the genus *Dicella* (Fritz Müller, Solereder, Niedenzu, Chodat) and in *Stigmaphyllon jatrophaefolium* (Chodat). According to Chodat, it is given off internally by the cambium in both genera.

A series of Malpighiaceous lianes possess stems with a lobed or grooved xylem-mass (Fig. 37, *A*). In these plants bast-tissue fills the grooves of the xylem, which are lined by the cambium; sometimes (*Heteropteris*) there are superficial grooves on the stem corresponding to the largest grooves of the xylem. Stems of this kind are found in the genera *Tetrapteris*, *Heteropteris*, and *Peixotoa*.

The anomaly in question was figured by Jussieu in the first two of these genera (Pl. III, Fig. 4 and Fig. 7, 8). The piece of stem of *Heteropteris intermedia*, Griseb., collected by Schenck, which is 4 cm. in thickness and is represented in his Fig. 58, Taf. VI, only shows indications of the anomaly. It appears more distinctly in a piece of stem belonging to *Heteropteris megaptera*, Juss., which is 9 cm. thick, and is figured by Schenck in Fig. 59, Taf. VI. H. Schenck also refers a piece of stem (No. 482 of his collection), which shows the same anomaly, and which he has represented in Fig. 60, Taf. VI, to *Heteropteris* and probably also the liane mentioned by Wigand (Flora, 1856, Taf. VII and p. 675). Probably most of the species of *Tetrapteris* from a certain age onwards possess a grooved xylem-mass. In older stages of the stem of *Tetrapteris* we find associated with the grooving a second anomaly, the subsequent splitting of the xylem-mass, which will be discussed below. H. Schenck described grooving alone in a stem of *Tetrapteris lucida*, Juss., 2½ cm. in thickness and a stem of *T. glabra*, Griseb., 2 cm. in thickness. Grooving is mentioned as occurring in *Peixotoa* by Fritz Müller[1] (Bot. Zeitung, 1866, p. 58, Taf. VII, Fig. 2).

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[1] The deeply-grooved stem of a liane figured by Niedenzu in the Natürl. Pflanzenfam., loc. cit., in Fig. 37, A–B on p. 44 and described as *Banisteria* sp., does not belong to the Malpighiaceae, as H. Schenck has already mentioned, and as may be repeated here in consideration of the wide circulation of Engler and Prantl's work, but possibly to the Apocynaceae or Hippocrateaceae. It is true that intraxylary phloem, which occurs in the Apocynaceae, could not be demonstrated in this piece of stem, as the pith and the innermost parts of the wood had perished, but elements resembling laticiferous tubes are present, and give rise to a web ('Spinnen') on breaking the cortex, and these occur in both the Orders last named.

Stems with lobed or grooved xylem-mass and with subsequent fission of the xylem are stated by H. Schenck to occur in the genera *Tetrapteris* (pro parte), *Mascagnia*, *Mezia* and *Banisteria*. This fission of the xylem is initiated by the formation of the grooves, and takes place chiefly in the radial direction, but may at the same time occur in a tangential direction.

The species concerned are: *Tetrapteris Guilleminiana*, Juss. (loc. cit., Taf. VI, Fig. 62, *a–c*), *T. inaequalis*, Cav. (loc cit., Taf. VI, Fig. 65). *Tetrapteris* sp. (loc. cit., Taf. VI, Fig. 66, *a*, *b*, reproduced in our Fig. 37, *B*), *T. multiflora*, Juss.; *Mascagnia* sp. (loc. cit., Taf. VI, Fig. 67, *a*); *Mezia Araujei*, Schwacke (loc. cit., Taf. VI, Fig. 68); *Banisteria* (?) *macrophylla*, Juss. (loc. cit., Taf. VII, Fig. 69), *B. argentea*, Spreng., *B. Riedeliana*, Regel, *B. nigrescens*, Juss. (according to Jussieu, Taf. III, Fig. 6, h_4).

The genus *Stigmaphyllon* shows the last and at the same time most highly differentiated type of anomaly. Here the wood at first grows in thickness by a normal cambium, which is not undulated, and is enclosed in a normal manner by a broad zone of phloem. The wood contains abundant wood-

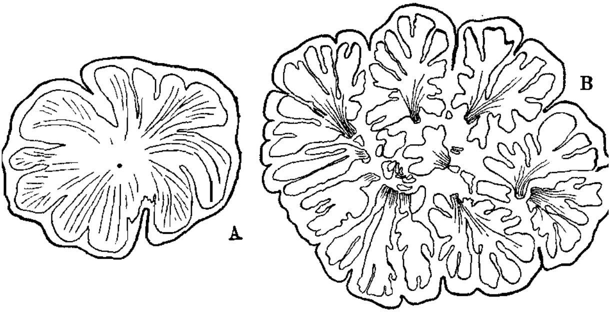

FIG. 37. A, Grooved stem of *Heteropteris*, sp. (Schenck, Holzs. no. 487, Rio). B, Stem with split xylem of *Tetrapteris*, sp. (Schenck, Holzs. no. 500, Rio). Both transverse sections approximately natural size.—After H. Schenck.

parenchyma and broad medullary rays, both having thin walls; owing to this the hard elements of the wood appear broken up into strands. Sooner or later, in consequence of cell-division in the parenchymatous tissue, new cambial layers are formed in connexion with these strands, and produce new bundles of wood and bast.

Jussieu first observed this anomalous structure in *Stigmaphyllon acuminatum* (loc. cit., p. 113, Plate III, Fig. 2); according to Jussieu the same anomaly also occurs in *S. Finlayanum*, *S. affine*, *S. ciliatum* (in the latter according to De Bary also, but the correctness of his determination is doubtful according to H. Schenck) and in *S. Gayanum*. H. Schenck has fully discussed the anomaly in question in *S. acuminatum*, Juss. (see also his Figs. 70, 71 on Plate VII), and has observed it in stems of *S. puberulum*, Griseb., and *S. tomentosum*, Juss. 2–2·5 cm. in thickness.

It may be added that the anomalies last described only appear in rather thick axes, and are therefore not present in herbarium-material, while the islands of soft bast in *Dicella* are to be met with in the branches found in herbaria.

It may also be mentioned that some of the Malpighiaceous lianes, e.g. species of *Hiptage*, *Schwannia*, *Thryallis*, *Tetrapteris* pro parte, and *Heteropteris* pro parte, have been proved to have normal structure (H. Schenck).

Literature: Gaudichaud, in Guillem. Arch. bot., t. ii, 1833, p. 502, t. 119.—Jussieu, Compt. rend., t. xii, p. 541, in Ann. sc. nat., sér. 2, t. xv, 1841, p. 234 and Arch. Mus. d'hist. nat., t. iii, 1843, p. 100 et seq.—Crüger, Bot. Zeit., 1850, p. 97 et seq.—Wigand, Flora, 1856, p. 673, Fig. 7.—Fritz Müller, Bot. Zeit., 1866, p 59.—Martinet, Org. de sécrét., Ann. sc. nat., sér. 5, t. xiv, 1872, pp. 183–5 and pl. 18.—Möller, Denkschr. Wiener Akad., 1876, pp. 88 and 384.—Vesque, Anat. de l'écorce, Thèse, Paris, 1876, pp. 90, 91.—Möller, Rindenanat., 1882, pp. 271–3.—Radlkofer, Abh. naturw. Ver. Bremen, Bd. viii, 1883, p. 378.—Solereder, Holzstr., 1885, pp. 88–90.—Witte, Lianen, Diss., Freiburg i. Br. u. Kiel, 1886, pp. 4–10.—Niedenzu, Ber. deutsch. bot. Gesellsch., 1890, pp. 190–4 and in Natürl. Pflanzenfam., 3. Teil, Abt. 4, 1890, pp. 42–44.—Chodat, Arch. sc. phys. et nat., sér. 3, t. xxvii, Genève, 1892, p. 229 et seq. and Atti del Congresso bot. internaz., 1892, p. 144 et seq.—H. Schenck, Anat. d. Lianen, 1893, pp. 110–25, Taf. vi, vii.—H. Schenck, Zerklüftungsvorg., Pringsheim Jahrb., Bd. xxvii, 1895, p. 607 et seq.

ZYGOPHYLLEAE.

According to the general preliminary investigations hitherto made, the simple perforations of the vessels, the wood-prosenchyma provided with bordered pits, and the absence of special subsidiary cells accompanying the stomata are characteristic of this Order. In the branch the boundary between bast and primary cortex is formed by isolated groups of primary bast-fibres, between which, according to Engler, groups of stone-cells are sometimes intercalated; the latter occasionally also appear in the primary cortex. In the secondary bast, fibres are completely wanting.

The **hairy covering** consists of ordinary simple unicellular hairs, more rarely of unicellular two-armed hairs; Engler states that the latter occur in the section *Agrophyllum* of the genus *Zygophyllum* (formerly an independent genus). The two forms of hair are connected by the one-armed unicellular hairs, which have been observed by Volkens in *Nitraria retusa*, Aschers. The ordinary unicellular hairs either have thick walls and narrow lumina, e.g. in *Porlieria hygrometra*, Ruiz. et Pav., or thin walls and relatively wide lumina, e.g. in *Larrea divaricata*, Cav. (Fig. 38, *A*); in this latter species they are attenuated and pointed both towards the tip and towards the base. A special modification of the ordinary simple unicellular type is found in those hairs which, according to Volkens, give the leaves of the species of *Fagonia* a glandular and sticky appearance. They can be divided into two groups—those in which the secretion exudes from the cavity of a thin-walled hair-cell (*Fagonia latifolia*, Del., *F. kahirina*, Boiss., *F. Bruguieri*, DC., *F. mollis*, Del.), and those in which the secretion is apparently produced by the metamorphosis of the thickened wall of the hair (*F. arabica*, L., Fig. 38, *B*; *F. glutinosa*, Del.). The secreting cells are in all cases found on the apices of small elevations of the leaf-surface. Glandular hairs, other than those just described, do not occur in the Order. The resinous excretions, which cover the branches and leaves of *Larrea mexicana*, Moric., the well known desert-shrub, are not the product of external glands, but, according to Volkens, of the inner (i.e. upper) epidermis of the stipules, which is differentiated like a tesselated epithelium.

Oxalate of lime is, for the most part, present in the leaves in the form of clustered crystals, in the axis in the form of ordinary solitary, or clustered crystals. But besides these, two other forms of deposition have been observed, namely, styloids of more or less typical shape (in the bast of *Guaiacum officinale*, L., Fig. 38, *C*; *Porlieria hygrometra*, Ruiz. et Pav., and *Larrea mexicana*, Moric.; see Holzner, Möller, Solereder, and Radlkofer) and small acicular crystals (according to my own observations in the bast and leaf-tissue of *Nitraria Schoberi*, L., and in the bast and primary cortex of *Tribulus terrestris*, L.).

To the preceding description of the specially important anatomical features I may add the following detailed statements regarding the structure of the leaf and branch.

The **leaf-structure** is centric in *Guaiacum officinale*, *Larrea divaricata*, and *Porlieria hygrometra*, and likewise in *Tribulus alatus*, Del., species of *Fagonia*, and *Zygophyllum*, and *Nitraria retusa*, Aschers., according to Volkens. In the acicular leaves of *Zygophyllum album*, L. and other species, the middle of the leaf, according to the same author, is occupied by a central thin-walled aqueous tissue, which surrounds the vascular bundle. The large colourless water-cells, which, according to Volkens, are found in *Nitraria retusa* scattered in the mesophyll (consisting only of palisade-tissue) are, as my own investigation proved, mucilage-cells with their membranes mucilaginous on all sides and

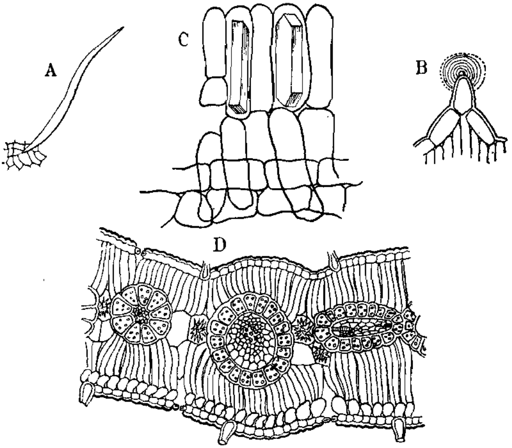

FIG. 38. A, Hair of *Larrea divaricata*, Cav. B, Glandular hair of *Fagonia arabica*, L. C, Crystal-cells from the bast of *Guaiacum officinale*, L. D, Transverse section of the leaf of *Tribulus alatus*, Del.—A, Original; B and D after Volkens; C after Möller.

clearly stratified. In *Tribulus alatus*, the lowermost cell-layer of the mesophyll consists of colourless cells with incurved outlines. In *Guaiacum officinale*, *Larrea divaricata*, *Porlieria hygrometra*, and *Zygophyllum simplex* the epidermal cells have a polygonal outline in surface-view. The stomata in these four species are present on both sides of the leaf. *Nitraria retusa* is characterized by a coating of wax on the surface of the leaf. In *Guaiacum officinale* every cell of the epidermis on both sides of the leaf contains a small doubly refracting crystal. The leaves of *Pintoa chilensis* bear black dots on the lower side, according to Engler. Each of these small black spots consists of a few large thin-walled cells, lying under the epidermis, and of a few smaller cells which belong to the epidermis itself and have brownish contents. In this connexion we may mention Engler's observation, that in the cells (*Fagonia*) or in the

intercellular spaces (*Nitraria, Zygophyllum cornutum*) of several members of the Order inhabiting saline soil, radially crystalline masses of variable size and consisting of some salt are met with; these bodies dissolve in hydrochloric, acetic, and nitric acids. In *Tribulus alatus* the vascular bundles of the veins up to their last ramifications are enveloped in characteristic sheaths of pitted cells with wide lumina and fairly thick walls (Fig. 38, *D*).

The **petiole** has only been investigated in *Tribulus terrestris, Guaiacum officinale*, and *G. arboreum*, by Petit. In *Tribulus* five isolated vascular bundles are found in the initial, and the same number in the characteristic; but these are not the same bundles, for splitting and fusion of the original five take place in their course through the petiole. In the characteristic region of the species of *Guaïacum* named a ring of wood and bast occurs, and above it one vascular bundle on each side.

As regards the structure of the **cortex**, the cork arises in the epidermis in *Guaiacum officinale*, according to Möller, subepidermally in *Porlieria hygrometra*, according to Douliot. In *Bulnesia Retamo* the pith contains stone-cells (Engler). The **wood**, which has been investigated in species of *Guaiacum, Larrea* and *Porlieria*, possesses narrow 1–2-seriate medullary rays. Tier-like structure of the medullary rays is described by Höhnel in the wood of the stem in *Guaiacum officinale* and *Porlieria hygrometra*. The vessels bear small bordered pits on those walls which adjoin medullary rays. In *Zygophyllum arboreum* carbonate of lime has been observed in the vessels of the heart-wood (Molisch). The wood-parenchyma is developed in varying abundance (cf. Möller's statements regarding *Guaiacum*). In *Larrea divaricata* and *Porlieria hygrometra* starch-containing fibrous cells are present in abundance in the wood.

Lastly, it remains to mention that special secretory receptacles are wanting in this Order; i. e. apart from the mucilage-cells described above and the enlarged cells with brown, tanniniferous contents, which are sometimes met with in the leaf-tissue, e.g. in *Nitraria retusa*. The resin to which the pharmaceutical use of *Guaiacum*-wood is due, fills the vessels of the heart-wood.

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GERANIACEAE.

1. Review of the Anatomical Features. The Geraniaceae have no special type of stomatal apparatus. The hairy covering consists of simple unicellular or uniseriate hairs, of bladder-hairs, and of glandular hairs with a uniseriate stalk and unicellular head (Fig. 39, *B*). Oxalate of lime occurs in the form of ordinary solitary crystals, clustered crystals, and raphides (the raphides in *Impatiens* only). Internal secretory organs are represented by schizogenous secretory cavities (in certain species of *Oxalis*) and also by cells containing a secretion (branched tannin-sacs in the spongy parenchyma of *Impatiens Sultani*, long tubular tannin-sacs in the epidermis on the lower side of the leaf in *Limnanthes Douglasii*, R. Br., secretory cells in the leaf-tissue of *Tropaeolum pentaphyllum*, Lam., and myrosin-cells in *Limnanthes* and *Tro-*

paeolum). The perforations of the vessels are simple ; the wood-prosenchyma, which is sometimes septate, generally bears simple pits. The boundary of primary cortex and bast is either formed by a composite and continuous ring of sclerenchyma, or by a ring of bast-fibres, or by isolated groups of bast-fibres. The cork arises (in *Monsonia*) in the outermost cell-layer of the primary cortex.

The following are specially noteworthy anatomical features in the Order: the occurrence of isolated annular and spiral vessels in the pith in species of *Impatiens* ; the medullary vascular bundles in the stem of certain species of *Geranium* ; the peculiar thickening-ridges, showing reticulate arrangement, in the cells of the subepidermal layer in the root of many species of *Erodium, Geranium*, and *Pelargonium* (Fig. 39, *C*).

2. Structure of the Leaf. The leaf-structure has been very incompletely investigated. From the statements of the authors and from some few observations of my own [1] the following remarks may be made on this subject. In *Oxalis carnosa*, Mol., the upper **epidermis** consists of very high cells elongated like palisade-tissue many times exceeding the remainder of the leaf-tissue in thickness, and serving for the storage of water ; in *O. arbuscula*,

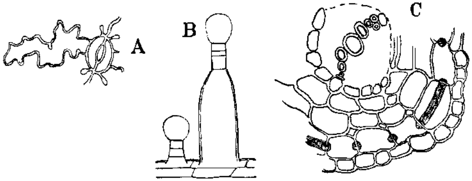

Fig. 39. A, Stoma of *Geranium Londesii*. B, Glandular hair of *Geranium favosum*, Hochst. C, Transverse section through a young root of *Geranium dissectum*.—A and C after Bergendal; B, original.

Barn., the epidermal cells on both sides of the leaf are arched outwards as papillae, but in *O. Inesitae*, Phil., only those of the upper side (Reiche). The **stomata** do not possess any special subsidiary cells. They are present either on both surfaces of the leaf (e.g. in *Pelargonium glechomoides*), or only on the lower side (*Viviania marifolia, Impatiens Sultani*, &c.). In *Erodium cicutarium, Geranium Londesii* (see Fig. 39, *A*), &c., according to Bergendal, curious projections, which are often T-shaped, are borne by the walls of the lower epidermal cells, mainly in the immediate neighbourhood of the stomata, but also elsewhere ; not uncommonly they are quite similar to those which have been described by Cohn and Weiss in the epidermal cells of the petals in different plants. In *Oxalis* the stomata are depressed ; according to Hildebrand, the distribution of the stomata on the leaves of *Oxalis*, shows a relation to the sleep-position of the leaves. **Water-pores** are present (Hermann) on the peculiarly constructed leaf-teeth of *Impatiens* ; they are likewise present above the terminations of the vascular bundles in the leaves of *Tropaeolum majus*, L.

The **hairy covering** consists of simple unicellular hairs (*Viviania marifolia*) or uniseriate hairs (*Geranium favosum*). Besides these, in *Oxalis carnosa* and other species, there are water-storing bladder-hairs (epidermal cells developed like bladders, according to Goebel and others), and in *Erodium, Geranium, Oxalis*, and *Pelargonium* there are glandular hairs with a stalk of variable

[1] The latter relate to *Geranium favosum*, Hochst., *Pelargonium glechomoides*, Rich., *Limnanthes Douglasii*, R. Br., *Viviania marifolia*, Cav., *Oxalis Acetosella*, L., *Impatiens tinctoria*, Rich.

length and a unicellular spherical head. The stalk of the glandular hair is unicellular or uniseriate, and in the latter case sometimes (*Pelargonium glechomoides*, Rich.) shows a certain amount of differentiation, the basal part being developed like a pedestal. According to Hanstein, the same kind of glandular hairs are also met with as a bud-protection in *Geranium* and *Pelargonium*, and had previously been mentioned by Martinet in numerous species of *Erodium*, *Geranium*, and *Pelargonium*. In connexion with the glandular hairs the glandular leaf-teeth of *Geranium Robertianum*, and of species of *Impatiens*, may be shortly mentioned. Of these the latter are often beset with small flask-shaped glandular structures, which, moreover, sometimes occur in other positions also, e.g. on the stem of *Impatiens parviflora*. For the detailed structure of these glandular leaf-teeth we may refer to Reinke's work (loc. cit.), and it is only necessary to make the general statement that the structures in question contain the terminations of veins, and include cells with special (in some cases mucilaginous) contents, and in addition to these raphide-sacs in *Impatiens*; their epidermis, which sometimes shows a special structure, bears stomata in *Geranium Robertianum* only.

Oxalate of lime is present in the form of clustered crystals, solitary crystals and raphides. *Viviania marifolia* contains numerous groups of relatively small clustered crystals in its palisade-tissue. In *Oxalis delicatula*, Pohl, as shown by a casual examination, clustered crystals also occur in the mesophyll, and give rise to very numerous distinct transparent dots. The small but very distinct pellucid dots in the leaf of *Oxalis laxa*, Hook. et Arn., on the other hand, are due to crystal-sacs, each of which contains a large solitary crystal, sometimes accompanied by smaller crystals. Raphide-sacs are characteristic of the genus *Impatiens*; they have been demonstrated by Blenk in no less than sixty-two species; they sometimes cause transparent dots in the leaf, and occur also in the stem. The raphide-sacs are characterized by mucilaginous contents. In *Impatiens tinctoria* I observed two kinds of raphide-sacs: firstly, such as contain short raphides and much mucilage, and secondly, others with a long bundle of raphides and scanty mucilaginous contents. In the leaf of *Limnanthes Douglasii*, no excretion of oxalate of lime takes place. Spindle-shaped protein-bodies are met with in some of the species of *Impatiens*, but not always in all the organs (Amadei).

Among the **secretory organs** we may specially mention the schizogenous secretory cavities, filled with brown or red contents which are occasionally transparent and crystalline; these cavities occur in many Cape and American species of *Oxalis*, and De Bary and Höhnel have already given data concerning them.

An investigation of the distribution and systematic value of these secretory cavities has still to be made. On examination with a lens or even with the naked eye they appear as small brown or reddish striae and are mentioned in descriptive botany as glands or small warts. They are, as a rule, found on the leaf-margin, but in the case of narrow pinnules (e. g. of *Oxalis goniorhiza*, Eckl. et Zeyh. var. *β*, *semiglauca*, Sond., *O. pentaphylla*, Sims, *O. versicolor*, L., &c.), as I may mention from a casual observation, they lie two together at the apex of the usually emarginate pinnule. In *O. Martiana*, Zucc., the brown dots are present in very large numbers on the whole surface of the pinnule; the same is sometimes the case, but not on all of the leaflets, in *O. ornata*, Poepp. The secretory cavities in question have been investigated in somewhat greater detail by Höhnel in *Oxalis pentaphylla*, Sims, and *O. floribunda*, Lehm. In the first named species, in which the secretory cavities, as already stated, occur in pairs at the apex of each pinnule, the glandular space is closed on all sides and lined by a well differentiated epithelium. In *O. floribunda*, on the other hand, where as many as thirty dot-like or linear warts of various sizes are distributed over the whole surface of each leaflet, the epithelial cells are scarcely distinguished from the surrounding cells of the mesophyll, and in this case only the younger secretory cavities are provided with a closed epithelium;

when they are older the epithelium is burst owing to the accumulation of secretion, and hence the secretory space communicates with the air-containing intercellular spaces of the leaf. In both the species in question the red secretion, according to Höhnel, is crystalline, forming a sphere-crystal in the smaller glands in just the same way as in the secretory cavities of the Myrsineae and species of *Lysimachia*, while in the linear warts, on the other hand, it forms a more granular mass, which is soluble in alcohol, ether, acetic acid, potash solution, &c. According to Hildebrand, the secretory cavities also occur in the bulb-scales and petals of the species of *Oxalis* referred to.

A second type of internal secretory element is found, according to Hermann, in *Impatiens Sultani*. The spongy parenchyma of this species contains cells branched in a dendritic manner and spread out in the direction of the leaf-surface; these cells contain tannin. Special tannin-containing cells, according to Guignard, also occur in *Limnanthes* (*L. Douglasii*, R. Br.). They are long tubular cells occurring in the lower epidermis, and attaining a length of ·2 to 2.5 mm.; they are elongated parallel to the long axis of the leaf-tips, and sometimes lie in twos with their longitudinal walls touching; cells of a similar nature occur in the epidermis of the branch or immediately in contact with it. Spherical secretory cells of inconsiderable size (diameter = ·015 mm.) are stated by Blenk to occur in the leaf-tissue of *Tropaeolum pentaphyllum*, Lam. These give rise to extremely delicate dots, which only become visible with a lens. Their contents are doubly refractive, do not stain with iodine-solution, are insoluble in alcohol, ether, and glycerine, but are soluble in water, and in dilute potash-solution. The sphaerocrystalline masses, which Blenk met with in certain leaves of *Tropaeolum majus*, var. *fuscum*, appear to consist of the same substance.

Lastly, myrosin-cells, which have already been described as occurring in the Capparideae and their allies, reappear in the Geraniaceae; although usually they only become evident on the employment of chemical reactions.

Myrosin is present in *Tropaeolum*, not only in the seed, as Spatzier mentions, but, according to Guignard, also in the vegetative organs, as might be inferred from their cress-like smell and taste. Guignard also succeeded, though Spatzier failed, in determining the localization of the myrosin in *Tropaeolum majus* and *T. peregrinum* with the help of Millon's reaction; it occurs in the bast and primary cortex of the root, and sparingly in the bast, but more abundantly in the subepidermal layer of the branches, and lastly, also in the tissue of the leaf. In the root and branch only certain cells give the reaction; sometimes they differ in their size from the neighbouring cells, so that one may speak of the occurrence of special 'myrosin-cells' in these tissues. In the leaves, on the other hand, distinct myrosin-cells are not evident; the myrosin appears to be distributed in the leaf in small quantities throughout a large portion of the tissue. Apart from *Tropaeolum*, myrosin-cells have also been observed by Guignard in the genus *Limnanthes* (*L. Douglasii*). Here they occur in the lacunar primary parenchyma of the cortex and in the endodermis of the root, as well as in the lacunar primary cortex and the bast of the branches, while in the leaf they are absent.

The structure of the **petiole** has been investigated chiefly by Petit, and in the case of the genera *Geranium*, *Pelargonium*, *Impatiens*, and *Erodium* also by Jaennicke, Bergendal, and Hermann. Petit's are the most important observations, and form the principal source of the following statements.

In the tribe Geranieae, Petit investigated the genera *Biebersteinia*, *Monsonia*, *Geranium*, and *Erodium*. These agree, in the following points: three vascular bundles enter the petiole, and the characteristic region contains a circle of four or more isolated bundles, of which usually four principal bundles appear orientated in an orthogonal cross. The detailed course of the vascular bundles in the petiole cannot be fully discussed here; it must suffice to mention that of the three bundles found in the initial region the lateral strands divide, and two of the vascular bundles thus produced are fused in the characteristic region to form the median

upper bundle. The species *Geranium anemonaefolium*, previously investigated by Bergendal, exhibits in the characteristic region an outer circle of fourteen smaller isolated vascular bundles and an inner circle of five larger ones; of these the two upper bundles are closely approximated; this structure may be derived from the type described. According to Jaennicke, the occurrence or absence of a pericyclic sclerenchyma-ring in contact with the vascular bundles is of importance for characterizing the species of *Geranium*; this sclerenchymatous ring is either entirely composed of hard bast-fibres (*G. phaeum*, *Pelargonium Andrewsii*, and the *pratense*-group) or consists of hard bast and stone-cells (*G. sanguineum* and *G. aconitifolium*). Of the tribe Pelargonieae, *Pelargonium* as well as *Tropaeolum* have been investigated. *Pelargonium* approaches the Geranieae in so far as three vascular bundles pass into the petiole; the characteristic region exhibits a circle of six or more isolated bundles—which are applied to a pericyclic ring of hard bast or to a composite sclerenchymatous ring—and besides these a central medullary bundle, which according to Jaennicke and Petit is characteristic of the genus. *Tropaeolum* shows different features; in the initial region a circle of eight isolated bundles is found, in the characteristic region, a circle of nine bundles. The latter region in *Viviania petiolata*, belonging to the tribe Vivianieae, possesses an arc-shaped vascular system and one small vascular bundle on each of its flanks; the investigated species of *Wendtia* and *Rhynchotheca* (tribe Wendtieae) contain only one well-developed vascular bundle in this region. Of the Oxalideae species of *Oxalis* and *Averrhoa* have been investigated, of the Balsamineae species of *Impatiens*. In *Oxalis tetraphylla*, Cav., the initial region of the petiole has an arc of nine isolated bundles, while the characteristic region shows a ring of wood and bast, which encloses two medullary bundles; in this region *Oxalis latifolia*, H. B. K., has an interrupted ring of bundles and no medullary bundles, *Averrhoa Carambola* has a ring of wood and bast, while *Impatiens* has an arc formed of three bundles.

3. Structure of the Axis. Concerning the structure of the **wood** in the woody species, my earlier general investigation, which extended to species of the genera *Monsonia*, *Pelargonium*, *Viviania*, and *Averrhoa*, gave the following results. Ray-parenchyma is absent in *Monsonia angustifolia*, E. Mey, and *Viviania marifolia*, Cav.; elsewhere the medullary rays vary in breadth; in *Averrhoa Carambola*, L. they are uniseriate or biseriate only. The vessels have simple perforations. In contact with parenchyma of the medullary rays the wall of the vessel shows simple pitting with transitions to bordered pitting. The pitted vessels of *Viviania marifolia* are spirally thickened. Wood-parenchyma is not conspicuously developed. The walls of the prosenchyma are, as a rule, provided with simple pits; in *Viviania* a distinct pit-border is present in most cases; the wood-prosenchyma of *Averrhoa Carambola*, L., is sometimes septate.

As regards the structure of the **cortex**, I may add that in *Monsonia angustifolia*, E. Mey, the boundary between the bast and primary cortex is formed by isolated groups of hard bast, and in *Averrhoa Carambola*, L., by a composite and continuous sclerenchyma-ring; in *Monsonia* the cork, which is composed of cells with wide lumina and thin walls, takes its origin immediately below the epidermis. The many-layered periderm of *Sarcocaulon rigidum*, Schinz, also deserves mention; it is filled with a wax-like substance, and at any rate has some connexion with the resinous covering of the branches (Volkens).

The following facts should be pointed out regarding the stem-structure of the **herbaceous species**. The genus *Impatiens* is specially interesting on account of the occurrence of isolated annular and spiral vessels in the pith [1], which are differentiated before the development of the vascular bundles (Beyse), and on account of the structure of the nodes of the stem, where the libriform of the xylem in the internodes is replaced by collenchymatous tissue. In *Impatiens* the innermost layer of the primary cortex is formed by a starch-

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[1] In *I. Balsamina*, *I. Noli-tangere*, and *I. parviflora*.

sheath which subsequently becomes a suberized endodermis. The firmness of the thick stems of certain species of *Impatiens*, which often attain the height of a man, is entirely due to the strongly turgescent ground-tissue. Of the genera *Geranium*, *Pelargonium*, and *Erodium*, the first two have a ring of hard bast in the pericycle. *Erodium*, on the other hand, has a composite and continuous sclerenchyma-ring (Jaennicke). In certain species of *Geranium* (*G. palustre*, *G. Robertianum*, and *G. sanguineum*) the fibro-vascular strands of the aerial parts of the stem, like those of the Cucurbitaceae, are arranged in two circles; those belonging to the inner circle may be regarded as medullary bundles, and some of them have concentric structure with central phloem (J. E. Weiss, Bergendal). The peripheral strands are the leaf-traces of the next pair of leaves above; the medullary strands are essentially the continuation of the fusing vascular bundles of the next higher internode.

As regards **the structure of the root**, the subepidermal layer of the main and lateral roots in the genera *Erodium*, *Geranium*, and *Pelargonium*, is distinguished by characteristic thickening-ridges. These occur on the horizontal and radial walls of the cells mentioned; they meet at the corners, and correspond in neighbouring cells, and thus form a network of rectangular meshes developed in the tangential direction (see Bergendal and Van Tieghem, loc. cit.).

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RUTACEAE.

1. Review of the Anatomical Features. The Rutaceae are characterized in a very definite manner by certain anatomical characters: firstly, by the presence of schizogenous secretory cavities in the ground-tissue of the branches and of the leaf, giving rise to transparent dots visible either in the uninjured leaf or on a cut surface; further, by the almost exclusive occurrence of simple perforations in the vessels, by the occurrence of bordered pits on the vessel-wall where it is in contact with parenchyma, as well as by the wood-prosenchyma with simple pits; **lastly, by the nature of the pericycle, which in the majority of the Rutaceae contains isolated groups of bast-fibres. Only**

a few members of the Order afford exceptions with respect to the features just mentioned: I. Secretory cavities are not present in *Phelline*, the systematic position of this genus, however, requires further consideration. II. In some few genera (*Leptothyrsa*, *Boenninghausenia*, *Calodendron*, *Adenandra*, *Barosma*, *Agathosma*, *Acronychia*, *Clausena*, *Paramignya*) scalariform perforations with few or many bars have been observed side by side with the simple perforations. III. In *Skimmia* and *Orixa*, relatively small simple pits are found on the vessel-walls where they are in contact with parenchyma. IV. A composite and continuous sclerenchyma-ring in place of the isolated primary bundles of bast-fibres has been observed only in *Amyris*, *Pilocarpus*, and *Paramignya*.

The following statements may be made regarding the remaining anatomical features. A special type of stoma usually does not appear in this Order. The origin of the cork is superficial. The special forms of hairs occurring are peltate (Fig. 41, *D*), tufted and stellate hairs, unicellular or multicellular glandular hairs of various forms (Fig. 41, *A–B*), and glandular warts containing a secretory space (*Dictamnus*, Fig. 41, *C*). Oxalate of lime is excreted in the form of ordinary rhombohedra or clustered crystals, but sometimes also in the form of raphides (*Erythrochiton*, *Galipea*, *Raputia*, *Ravia*) or styloids (*Erythrochiton*, *Galipea*, *Monnieria*, *Raputia*, *Ravenia*, *Ravia*) or of typical crystal-sand (*Cusparia*, *Orixa*).

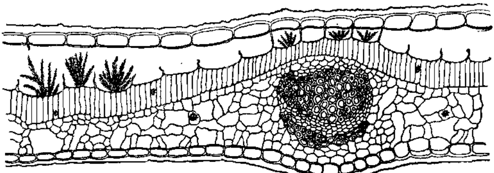

FIG. 40. Transverse section through the leaf of *Barosma serratifolia*, Willd.—Original.

Of special secretory elements we may also mention (*a*) the mucilage-cells or mucilage-spaces in the cortex of species of *Zanthoxylon*, *Evodia*, and *Phellodendron*, (*b*) the mucilage-cavities in the wood of *Evodia rutaecarpa*, Hook. f. et Thoms., (*c*) the central secretory canal in the pith of *Clausena punctata* (Retz.), (*d*) the resin-cells, which are present in very many members of the Order in the pith, primary cortex, parenchyma and medullary rays of the bast, and (*e*) the gelatinization of the epidermis of the leaf (Fig. 40), which occurs in certain species and is often present to a considerable extent. Hypoderm has been observed on the upper side of the leaves of *Cusparia cuneifolia*, Engl., and *Peganum Harmala*, L., papillose differentiation of the lower epidermis of the leaf in *Spiranthera odoratissima*, St. Hil.

2. STRUCTURE OF THE LEAF. Apart from the secretory elements, of which I shall speak later, little is known as to the leaf-structure of the Rutaceae The **epidermal cells** have straight or undulated lateral walls. Gelatinization of the inner membrane has been observed in the epidermis of *Toddalia aculeata*, Pers., *Empleurum ensatum*, Eckl. et Zeyh., and *E. serrulatum*, Ait, and is specially conspicuous in Buku-leaves (species of *Barosma*, see Fig. 40). In the case last mentioned the mucilage in the dried leaves frequently includes dendritic crystalline excretions of hesperidin, which dissolve in potash-solution with yellow coloration of the liquid. In *Cusparia cuneifolia*, Engl., a fairly large-celled hypoderm is found below the epidermis on the upper side of the leaf,

and a similar structure occurs in *Peganum Harmala*, L., according to Volkens; in *Spiranthera odoratissima*, St. Hil., according to Radlkofer, the epidermis on the lower side of the leaf shows papillose differentiation. The **stomata** are found either on both sides, e.g. in *Ruta graveolens*, L., or only on the lower surface of the leaf. They are, as a rule, not accompanied by any special subsidiary cells[1], but in *Cusparia cuneifolia*, Engl. one or two subsidiary cells, which are parallel to the pore, lie on either side of the guard-cells. The **veins** frequently contain sclerenchyma accompanying the vascular bundles, e.g. in *Cusparia cuneifolia*, sometimes, however, it is wanting (*Ruta graveolens*).

Oxalate of lime has been observed in the leaf in the form of ordinary solitary crystals, clustered crystals, raphides and styloids. Solitary crystals are found in *Citrus* accompanying the sclerenchyma of the veins as well as in enlarged epidermal cells of special form; in these only quite a small portion of the cell takes part in the formation of the outer wall of the epidermis, while its lower portion penetrates slightly into the assimilatory tissue of the leaf; in these epidermal cells the crystals are embedded in the strongly thickened inner membrane. Clustered crystals are very widely distributed in the mesophyll of numerous species (e.g. *Ruta graveolens, Cusparia cuneifolia, Toddalia aculeata*); sometimes they also occur accompanying the sclerenchyma of the veins. Blenk has demonstrated raphides in the leaf-tissue of *Erythrochiton brasiliensis*, Nees et Mart.; according to my own observations, styloids are found in *Monnieria trifolia*, L., and in a new, and as far as I am aware as yet undescribed, species of the same genus from Ecuador (Eggers, no. 14732). Lastly, we may mention the sphaerocrystals which Schaarschmidt met with in alcohol-material of *Haplophyllum Biebersteinii*, and described as behaving similarly to inulin; as also the sphaero-crystalline masses of oxalate of soda, which Blenk observed in the mesophyll in herbarium-material of *Malacocarpus* (*Peganum*) *crithmifolius*, Fisch. et Mey.

The following facts may be mentioned concerning the **hairy covering**. Glandular hairs are by no means found in all members of the Order; they are absent, e.g., in *Ruta graveolens, Cusparia cuneifolia, Diosma vulgaris*, Schlecht., and in other species. The structure of the glandular hairs varies. In *Monnieria* they are unicellular and club-shaped; here they chiefly occur above the secretory cavities. In *Toddalia aculeata*, Pers. (Fig. 41, *A–B*) the shortly stalked glandular hairs have a pear-shaped head composed of numerous polyhedral cells, and are sunk in small pits in the leaf. According to Rauter, club-shaped multicellular external glands are found in *Correa*. The external glands found on the surface of the leaf of *Dictamnus* have a 1–4-seriate stalk and a spherical multicellular head. The peculiar glandular warts (Fig. 41, *C*), which occur in the floral region of *Dictamnus* and enclose a secretory cavity, will be discussed more fully below in the section dealing with secretory cavities. The following forms of clothing hairs have been observed. Unicellular bristle-hairs have been met with by Rauter in *Dictamnus*. Tufted hairs, with short or long ray-cells, are found in *Boronia ledifolia*, J. Gay var. Stellate hairs are not uncommon in the Order and occur in the genera *Calodendron, Zieria, Eriostemon, Phebalium, Urocarpus, Asterolasia, Correa, Chorilaena*, and *Diplolaena*, according to Bentham and Hooker, as well as in *Pleurandropsis*, according to Baillon. The stellate hairs of *Correa* have been investigated in detail by Rauter; they possess a multiseriate stalk and a varied number of ray-cells. Peltate hairs occur in the genera *Eriostemon, Nematolepis, Phebalium, Rabelaisia* and *Urocarpus*, according to the statements of

[1] In *Ruta graveolens* the mother-cell of the guard-cells is cut off by the first and only division; in other words, the initial cell develops directly as the mother-cell of the guard-cells (see Strasburger, Pringsheim Jahrb., Bd. v, 1866–7, p. 304 and Taf. xxxvi).

systematists. The structure of the peltate hairs has been investigated in detail by O. Bachmann, but only in the genus *Phebalium* (Fig. 41, *D*), where it varies. The peltate hairs of *Phebalium Billardierii*, A. Juss., *P. glandulosum*, Hook., *P. rude*, Bartl., and *P. squamulosum*, Vent. have the same structure of the shield as in the Sterculiaceous genus *Heritiera*, since the ray-cells, which are free at the margin, only in part extend to the centre, and are more or less distinctly arranged in relation to a middle line; the stalk is short and consists of a layer of several cells. In *Phebalium argenteum*, Sm. (Fig. 41, *D*) the shield is differently constituted, being formed essentially of a double zone of rays, and thus resembling the peltate scales of the Bombaceae.

The **secretory cavities**, as is generally known, have been pointed out by

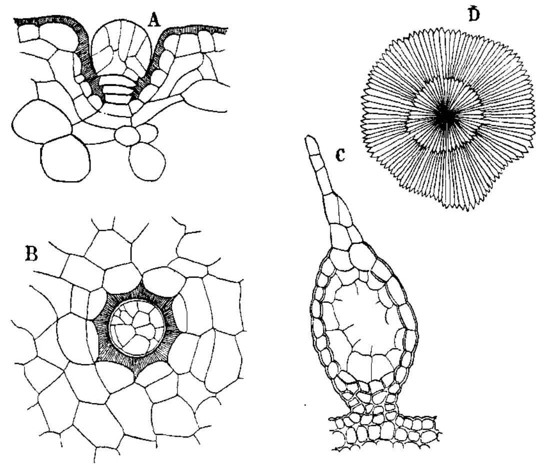

FIG. 41. A–B, Glandular hair from the leaf of *Toddalia aculeata*, Pers., A in section, B in surface-view. C, Glandular shaggy hair from the floral region of *Dictamnus Fraxinella*, Pers. D, Peltate hair of *Phebalium argenteum*, Pers.—A–B Original, C after Rauter, D after O. Bachmann.

Engler as an excellent systematic character for the delimitation of the Order. It is also well known that they give rise to transparent dots in the leaf, either in the uninjured leaf or on a cut surface; these dots are usually distributed uniformly over the whole leaf-surface, but are sometimes restricted to the margin. There are two opposite views regarding the origin of these secretory cavities: Rauter, Martinet, Chatin, De Bary, and Höhnel ascribe a lysigenous origin to them; Frank, Van Tieghem, and Leblois state that their origin is schizogenous. According to the most recent investigations of Sieck the truth probably lies between the two. The secretory cavities of the Rutaceae (and likewise the secretory receptacles of the Simarubaceae, Anacardiaceae, and Dipterocarpeae, as well as those of the genera *Liquidambar* and *Copaifera*) are schizolysigenous.

In the cases investigated by Sieck (species of *Amyris*, *Barosma*, *Citrus*, *Correa*, *Dictamnus*, *Ptelea*, and *Ruta*), the oil-cavities develop from the products of division of a specially characterized mother-cell, the daughter-cells separating schizogenously from one another in the middle. The walls of the daughter-cells, which abut on the secretory space and have the character of mucilaginous membranes, are, according to Sieck, the seat of the secretion. This secretion arises between an outer mucilaginous lamella and an inner lamella in the swollen, cap-shaped portions of the wall, which abut on the intercellular space. When the secretion accumulates in some quantity, the mucilaginous lamella bursts, and ultimately also the inner lamella; thereupon gelatinization of the middle lamellae of the lateral walls in the cells bordering on the cavity soon ensues: in short, solution of the cells surrounding the secretory space takes place, and this goes on, so that a lysigenous widening of the secretory cavity, which was first formed in a schizogenous manner, takes place.

The secretory cavities of *Haplophyllum tuberculatum*, A. Juss. are specially remarkable owing to their standing in relation to the water-conducting system; for tracheae branch off from the vascular bundles of the veins and run up to the glands. Special mention may now be made of the secretory cavities which occur in the wart-like trichome-structures of *Dictamnus* (see above and Fig. 41, *C*). Each of the latter, as Rauter has demonstrated, is a multicellular ovoid body, which arises from a single epidermal cell, and at its apex runs out into a single hair (biseriate at its base, but uniseriate above), while its lower part consists of a permanent peripheral layer of epidermal cells with scanty contents, and of an internal multicellular mass, rich in oil, and afterwards replaced by a secretory space.

The secretory cavities in question have been demonstrated by Engler, Möller, and Blenk in numerous members of the Order. Only in some few of the genera, cited in Bentham and Hooker, Gen. Plant., p. 279 et seq., was the absence of secretory cavities mentioned by the above observers, namely: *Erythrochiton*, *Hyptiandra*, *Melanococca*, *Peganum*, *Phelline*, and *Phellodendron*. But of these six exceptions, two, namely, *Erythrochiton* and *Phellodendron*, must be removed, inasmuch as Radlkofer succeeded in demonstrating secretory cavities in these also. Further, *Peganum*[1] does not come into consideration as an exception, because this genus, in accordance with the unanimous opinion of Engler, Baillon, and Eichler, must be included among the Zygophylleae; this also applies to the genus *Melanococca*, which, as is well known, has been shown by Engler to be a species of *Rhus*, and to the genus *Hyptiandra*, which in Bentham and Hooker's supplement has been appended to the Simarubaceae. Of all the genera investigated[2], *Phelline* thus remains the only real exception.

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[1] *Peganum crithmifolium*, Retz. has numerous raphide-sacs in its mesophyll. In *P. Harmala*, L. the cells of the mesophyll are entirely filled by numerous rod- and needle-shaped crystals, deviating from the raphide-type; in the medullary rays of the branches of *Peganum Harmala* bundles of short acicular crystals are also found, and some cells of the primary cortical parenchyma and especially those adjoining the epidermis, are crowded with acicular crystals, which are also present in the bast. Moreover, according to Höhnel, an abundant secretion occurs in the ordinary intercellular spaces of the leaf in *Peganum Harmala*.

[2] Blenk, Engler, and others have met with secretory cavities in the following genera of Rutaceae, which are cited in the serial order of Durand's Index:—Tribe I, Cusparieae: *Spiranthera*, *Almeidea*, *Leptothyrsa*, *Erythrochiton*, *Naudinia*, *Galipea*, *Raputia*, *Decagonocarpus*, *Cusparia*, *Ravia*, *Ticorea*, *Ravenia* and *Monnieria*; Tribe II, Ruteae: *Ruta*, *Boenninghausenia*, *Dictamnus*, *Tetradiclis*, *Thamnosma*; Tribe III, Diosmeae: *Calodendron*, *Euchaetis*, *Macrostylis*, *Diosma*, *Coleonema*, *Acmadenia*, *Adenandra*, *Barosma*, *Agathosma*, *Empleurum*; Tribe IV, Boronieae: *Zieria*, *Boronia*, *Acradenia*, *Eriostemon*, *Phebalium*, *Microcybe*, *Geleznovia*, *Crowea*, *Philotheca*, *Asterolasia*, *Correa*, *Nematolepis*, *Chorilaena* and *Diplolaena*; Tribe V, Zanthoxyleae: *Melicope*, *Evodia*, *Astrophyllum*, *Medicosma*, *Pitavia*, *Choisya*, *Zanthoxylon*, *Geijera*, *Pentaceras*, *Decatropis*, *Polyaster*, *Megastigma*, *Lunasia* (*Rabelaisia*), *Pilocarpus*, *Esenbeckia*, *Metrodorea*, *Peltostigma*; Tribe VI, Toddalieae: *Toddalia*, *Balfourodendron* (= *Esenbeckia Riedeliana*, Engl.), *Phellodendron*, *Hortia*, *Ptelea*, *Helietta*, *Acronychia*, *Skimmia*, *Casimiroa*; Tribe VII, Aurantieae: *Glycosmis*, *Amyris*, *Stauranthus*, *Micromelum*, *Triphasia*, *Limonia*, *Murraya*, *Clausena*, *Luvunga*, *Paramignya*, *Atalantia*, *Citrus* *Feronia* and *Aegle*. Among the remaining genera enumerated in Durand's Index, pellucid dots in the leaf are stated to occur in the following by the authors concerned, and are almost certainly due to secretory cavities, although an anatomical investigation has not been made: *Toxosiphon* (tribe Cusparieae); *Psilopeganum* (tribe Ruteae); *Zieridium* and *Boronella* (tribe Boronieae) *Bosistoa*, *Tetractomia*, *Brombya*, *Bouchardatia*, *Platydesma*, *Pagetia* (in which F. v. Müller

The **petiole** has been examined in only one or two genera (*Choisya, Dictamnus, Galipea, Pilocarpus,* and *Ruta*) by Petit and Plitt. In *Dictamnus Fraxinella* and *Choisya ternata*, according to Petit, three vascular bundles pass into the petiole. In *Choisya* these three bundles in their course through the petiole form three rings of wood and bast, and finally in the characteristic region constitute a single ring of wood and bast. In the latter region in *Dictamnus* a ring of wood and bast is met with, and at its centre a concentric vascular bundle with central bast and produced by the fusion of medullary bundles. The petiole of *Ruta graveolens*, according to Plitt, exhibits an almost closed arc of isolated vascular bundles, that of *Pilocarpus pennatifolius*, Lem. has a ring of wood and bast, and that of *Galipea ovata*, St. Hil. et Tul. a similar ring with medullary bundles.

3. Structure of the Axis. The account of the structure of the axis, which I give here, is based not only on the existing statements in the literature but also on my own more recent investigation of numerous Rutaceae[1], as to which Radlkofer has already published the most important results.

The following facts may be pointed out regarding the anatomy of the **wood** in this Order. Very broad medullary rays do not occur. The lumina of the vessels vary in size (maximum diameter = ·03–·15 mm.). The perforations of the vessels are exclusively simple in almost all the species. Scalariform perforations (with few, or numerous bars, which in the latter case are delicate) are only met with in a few species, side by side with the simple type; these species are: *Leptothyrsa Sprucei*, Hook. fil., *Boenninghausenia albiflora*, Reichb., *Calodendron capense*, Thunb., *Adenandra mundiaefolia*, Eckl. et Zeyh., *Barosma crenulata*, Hook., *Agathosma chortophila*, Eckl. et Zeyh., *Acronychia laurifolia*, Bl., *Clausena heptaphylla*, Wight et Arn., *Paramignya Griffithii*, Hook. fil. In all the Rutaceae, with the exception of *Skimmia* and *Orixa*, the walls of the vessels bear bordered pits where they are in contact with wood- or ray-parenchyma. Only in *Orixa* and *Skimmia* do small simple pits, of the size of the borders of the bordered pits, occur on these parts of the vessel-wall. Spiral striation or thickening of the vessel-wall has been observed in the following species: *Thamnosma montana*, Torr. et Frém., *Zieria cytisoides*, Smith, *Eriostemon myoporoides*, DC., *Philotheca australis*, Rudge, *Asterolasia correifolia*, Benth., *Evodia rutaecarpa*, Hook. fil. et Thoms., *Choisya ternata*, H. B. K., *Phellodendron amurense*, Maxim. The wood-parenchyma is either little developed or present in some abundance, e.g. in *Boronia ledifolia*, Gay, *Calodendron capense*, Thunb., or *Citrus Aurantium*, L.; it is septate and provided with solitary crystals in the chambers in *Ptelea*, *Citrus Aurantium*, *Murraya exotica*, L. The wood-prosenchyma, which forms the groundwork of the xylem (apart from the tracheides which are also present,

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Fragm. v, p. 178, probably incorrectly describes oil-cells as the cause of the transparent dots), *Orixa* (tribe Zanthoxyleae); *Pleiococca* and *Boninia* (tribe Toddalieae). No statements are to be found as to the occurrence of transparent dots or of secretory cavities in the genera *Pleurandropsis*, *Dutaillyea*, *Platydesma*, *Halfordia* and *Gonocitrus* cited by Durand, nor in the genera *Araliopsis*, Engl., *Sargentia*, Wats., *Tetracronia*, Pierre, *Thoreldora*, Pierre and *Toddaliopsis*, Engl., which have only been established recently. A detailed investigation of all these genera with regard to the particulars referred to is extremely desirable, while in the genus *Empleuridium*, which in its external morphological characters approaches the Celastrineae, 'folia epunctata' are stated to occur; this likewise requires a further examination.

[1] Above seventy species were examined belonging to the genera: *Spiranthera*, *Almeidea*, *Leptothyrsa*, *Erythrochiton*, *Galipea*, *Raputia*, *Cusparia*, *Ravia*, *Ravenia*, *Monnieria*; *Ruta*, *Boenninghausenia*, *Peganum*, *Dictamnus*, *Tetradiclis*, *Thamnosma*; *Calodendron*, *Euchaetis*, *Macrostylis*, *Diosma*, *Coleonema*, *Acmadenia*, *Adenandra*, *Barosma*, *Agathosma*, *Empleurum*; *Zieria*, *Boronia*, *Eriostemon*, *Phebalium*, *Microcybe*, *Crowea*, *Philotheca*, *Asterolasia*, *Correa*, *Diplolaena*; *Melicope*, *Evodia*, *Choisya*, *Zanthoxylon*, *Geijera*, *Pilocarpus*, *Esenbeckia*, *Metrodorea*, *Orixa*; *Toddalia*, *Phellodendron*, *Hortia*, *Ptelea*, *Acronychia*, *Skimmia*, *Casimiroa*; *Glycosmis*, *Amyris*, *Micromelum*, *Triphasia*, *Limonia*, *Murraya*, *Clausena*, *Luvunga*, *Paramignya*, *Atalantia*, *Citrus*, *Feronia*, *Aegle*.

e.g. in *Microcybe*, *Crowea*, *Choisya*, &c.), has simple pits or, at any rate, such as have only a narrow, usually indistinct border.

With regard to the structure of the **cortex**, it may firstly be pointed out that, according to the observations of Möller, Douliot, J. E. Weiss, Ross and others, the periderm always arises superficially, viz. immediately below the epidermis in *Citrus*, *Toddalia*, *Ptelea*, *Zanthoxylon*; in the epidermis in *Pilocarpus pennatifolius*, Lem., and *Eriostemon cuspidatum*, Cunn. The structure of the cork-cells varies. In *Zanthoxylon* the outer tangential walls are sclerosed. On the other hand, in the Rutaceous bark, probably erroneously described as *Esenbeckia* sp. in Möller's 'Rindenanatomie,' the sclerosis extends to the inner tangential walls. The cork-cells of *Ptelea trifoliata* have delicate walls. Phelloderm sometimes adjoins the cork-cambium on the inner side; it is thin-walled in *Zanthoxylon*, sclerotic in *Ptelea*. Lastly, in the cortex of *Esenbeckia febrifuga*, Juss. (the Brazilian Angostura-bark), a layer of from three to four rows of colourless cells forms the innermost part of the cork; these cells are stained a bright blue colour by oxidizing acids, which leads one to infer the presence of evodin, an alkaloid, which shows this chemical reaction (Oberlin and Schlagdenhauffen).

The nature of the pericycle is quite a special character in the cortex of most members of the Order. In most cases it contains isolated groups or bands of hard bast, in the neighbourhood of which, in certain species, single stone-cells or groups of stone-cells now and then occur, but in that case without the formation of a closed sheath of sclerenchyma. On the other hand, the occurrence of a composite and continuous ring of sclerenchyma, consisting of the primary groups of bast-fibres and intervening groups of stone-cells, is a rare phenomenon in the pericycle; I observed it only in the following species: *Pilocarpus subcoriaceus*, Engl., *P. spicatus*, St. Hil., *Amyris maritima*, Jacq., *Paramignya Griffithii*, Hook. fil., and *P. monophylla*, Wight[1]. The entire absence of sclerenchyma in the pericycle is equally rare and is seen in *Boenninghausenia albiflora*, Reichenb., *Coleonema pulchrum*, Hook., *Euchaetis elata*, Eckl. et Zeyh., *Skimmia laureola*, Sieb. et Zucc. (but not in *S. japonica*, Thunb., in which isolated groups of collenchymatous bast-fibres are present).

I subjoin a few special statements regarding the nature of the primary and secondary cortex. In *Almeidea rubra*, St. Hil., the primary cortex contains numerous stone-cells; in *Cusparia ovata*, Engl., and *Ravenia infelix*, Vell. it contains abundant sclerosed parenchyma with wide lumina, and in *Metrodorea pubescens*, St. Hil. et Tul., numerous sclerenchyma-cells, which have fairly wide lumina and are slightly branched. Development of hard bast in the secondary phloem is not uncommon (*Euchaetis elata*, Eckl. et Zeyh., *Acmadenia juniperina*, Bartl. et Wendl., *Barosma crenulata*, Hook.); it is sometimes arranged in the form of bands in the transverse section of the branch (*Evodia erythrococca*, F. v. Müll., *Choisya ternata*, H. B. K.) or forms complete rings (*Glycosmis pentaphylla*, *Correa*, *Murraya exotica*, L.). In *Evodia rutaecarpa*, Hook. f. et Thoms., in addition to bundles of bast-fibres, groups of stone-cells occur in the secondary bast.

The **secretory organs** and the features presented by the crystals in the axis deserve fuller treatment. With respect to the former it may first be pointed out that the characteristic secretory cavities, already mentioned in the section on the leaf-structure, are also present in the ground-tissue of the axis. They probably always occur in the primary cortex, sometimes in the pith also (*Galipea jasminiflora*, Engl., *Raputia alba*, Engl., *Ravia resinosa*, Nees et Mart., in the last-named species in the form of short canals).

[1] The same structure is shown by the genus *Peganum*, which, however (see p. 178), probably belongs to the Zygophylleae.

On the other hand they are completely absent in the wood and bast, and according to Van Tieghem they are likewise entirely wanting in the roots. In addition to secretory cavities other elements of the same nature occur in the axis, namely secretory cells, mucilage-spaces, and in one case, *Clausena punctata* (Retz.), secretory canals. The secretory cells were first observed by Möller in certain species; I have been able to demonstrate them in a very large number of species, which may be enumerated in a note [1]. In a transverse section of the branch they strike the eye on account of their rather large lumina and their oily or resinous contents; they are found in the bast (viz. in the parenchyma and especially in the medullary rays of the bast) in the primary cortex and sometimes also in the pith. In the bast-parenchyma they are frequently elongated in the vertical direction to a considerable extent, and now and then several of them are ranged one above another in the same direction. The mucilage-spaces (formed by cells with gelatinized membranes) occur in the primary cortex in certain species of *Zanthoxylon, Evodia,* and *Phellodendron* (*Zanthoxylon Budrunga*, Wall., *Z. obscurum*, Engl., *Z.* (?) sp. Balansa, Pl. Parag., No. 3255; *Evodia rutaecarpa*, Hook. fil. et Thoms.; *Phellodendron amurense*, Rupr.[2]). Moreover, in *Evodia rutaecarpa*, mucilage-cavities are found in the wood of branches, when sufficiently thick (radius of the wood = about 2.5 mm.); they arise by disorganization of wood-cells and are arranged in concentric circles. With regard to the occurrence of secretory canals in *Clausena punctata* (Retz.) it may be mentioned that in this species a single wide, apparently hysterolysigenous resin-canal is found in the centre of the pith.

With respect to the mode of excretion of **oxalate of lime** in the axis we may remark that this substance appears in the form of clustered crystals, ordinary solitary crystals, raphides, styloids, and crystal-sand. For example, *Ptelea trifoliata*, L., has clustered crystals in the primary cortex as well as in the bast (Möller). *Zanthoxylon fraxineum*, Willd. exhibits clustered crystals in the primary cortical parenchyma, and indistinct rhombohedra in the bast (Möller). According to the same author, the primary and secondary cortex in *Citrus Limonum* contains ordinary solitary crystals. To these statements I may first add that the clustered crystals of the bast of *Almeidea rubra*, St. Hil. are embedded in crystal-sand, and that in the primary cortex of *Evodia rutaecarpa*, Hook. fil. et Thoms., cells sometimes occur which, besides containing clustered crystalline bodies or solitary crystals, also include very numerous smaller crystals—a kind of coarse crystal-sand. I have met with raphides together with styloids in *Galipea jasminiflora*, Engl., *Raputia alba*, Engl., *Ravia resinosa*, Nees et Mart., and *Erythrochiton brasiliensis*, Nees et Mart., with styloids only in *Ravenia infelix*, Vell., and *Monnieria trifolia*, L. The two kinds of crystals last mentioned, raphides and styloids, occur in the pith, bast, and primary cortex of the species concerned; when raphides and styloids are found side by side in the same plant, the latter appear especially in the bast. Finally, typical sacs with crystal-sand are present in *Cusparia ovata*, Engl., and *Orixa japonica*, Thunb. In the first of these species many cells of the bast are filled with crystal-sand to such an extent that they are

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[1] *Ravia resinosa*, Nees et Mart.; *Ruta chalepensis*, L., *Boenninghausenia albiflora*, Reichenb., *Tetradiclis salsa*, Stev., *Thamnosma montanum*, Torr. et Frém.; *Coleonema pulchrum*, Hook., *Acmadenia juniperina*, Bartl. et Wendl., *Adenandra mundtiaefolia*, Eckl. et Zeyh., *Barosma crenulata*, Hook., *Agathosma chortophila*, Eckl. et Zeyh., *Empleurum serrulatum*, Ait.; *Zieria cytisoides*, Smith., *Boronia ledifolia*, Gay, *Asterolasia correifolia*, Benth., *Correa alba*, Andr.; *Melicope simplex*, Cunn., *Evodia erythrococca*, F. v. Müll., *Choisya ternata*, H. B. K., *Geijera salicifolia*, Schott, *Pilocarpus subcoriaceus*, Engl., *Orixa japonica*, Thunb.; *Toddalia aculeata*, Pers., *Ptelea trifoliata*, L., *Acronychia laurifolia*, Bl., *Skimmia japonica*, Thunb., *Amyris maritima*, Jacq. These secretory cells are present also in *Zanthoxylon Pterota*, H. B. K., where Trécul had already seen them, but interpreted them as secretory cavities.

[2] In *Phellodendron amurense* the mucilage-spaces were first observed and described by Höhnel.

visible even to the naked eye as white masses in a transverse section of the branch; bodies resembling clustered crystals are sometimes embedded in the crystal-sand. In *Cusparia ovata*, besides the crystal-sand, clustered crystals and rhombohedra are found in the cortex, and clustered crystals in the pith. In *Orixa japonica*, on the other hand, crystal-sand is the only form in which oxalate of lime is excreted, both in the pith and in the primary and secondary cortex.

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SIMARUBACEAE.

1. Review of the Anatomical Features. This Order is characterized anatomically by the following features: the absence of a special type of stomatal apparatus and of secretory cavities (in relation to the second character one must except the genera *Cneoridium*, *Dictyoloma*, and *Spathelea*, which possess secretory cavities and have recently been referred to the Rutaceae by Engler); the superficial development of the cork and the presence of isolated bundles of bast-fibres in the pericycle (exceptions: *Ailanthus*, *Alvaradoa*, *Balanites*, *Brunellia*, *Cadellia*, *Irvingia*, *Koeberlinia*, *Picramnia*, and *Quassia*, which possess a composite and continuous ring of sclerenchyma in this region); also the simple perforations of the vessels, the bordered pitting of the vessel-wall where it is in contact with parenchyma (exceptions in the latter respect: *Brunellia* and *Irvingia*); and the pits of the wood-prosenchyma, which either have no border or are only characterized by the presence of narrow borders. In a by no means small number of genera (*Ailanthus*, *Amaroria*, *Aruba*, *Brucea*, *Picraena*, *Picrasma*, *Picrocardia*, *Picrolemma*, *Simaba* pro parte, *Simaruba*, and *Soulamea*) resin-canals occur at the periphery of the pith but not in the cortex. In addition to this it may be mentioned that the genus *Koeberlinia*, which has recently been raised to the rauk of an Order (the Koeberliniaceae), possesses resin-canals in the bast but none in the pith.

The hairy covering is formed by simple unicellular trichomes—very rarely (*Cneorum*) by unicellular two-armed hairs—and by multicellular glandular

hairs of varied structure; but external glands do not occur in all the members of the Order. Oxalate of lime is usually excreted in the form of ordinary solitary and clustered crystals; in *Alvaradoa* styloids occur in the bast. Apart from the secretory canals and cavities already mentioned, the following secretory organs have been observed in the Order: mucilaginous epidermal cells; resin-cells (species of *Ailanthus, Cneoridium, Cneorum, Harrisonia, Picrella, Simaruba, Spathelea*); cells with gelatinized membranes in the cortical tissue (*Picrodendron Juglans*, Griseb.), and mucilage-spaces in pith and cortex (*Irvingia*). The secretory cells and cavities occasionally give rise to transparent dots in the leaf. Specially noteworthy specific characters in the structure of the leaf are: the papillose nature of the lower epidermis and the occurrence of sclerenchyma-fibres and of spicular cells in the mesophyll.

2. Structure of the Leaf. On this subject, only a few details are known from the literature, and from my own casual observations. In *Simaruba glauca*, DC., and *Simaba cuneata*, St. Hil. et Tul., the leaf-structure is bifacial. Papillose differentiation of the lower **epidermis** has been observed in *Simaruba glauca, Dictyoloma incanescens*, DC., and *D. peruvianum*, Planch., *Brunellia*

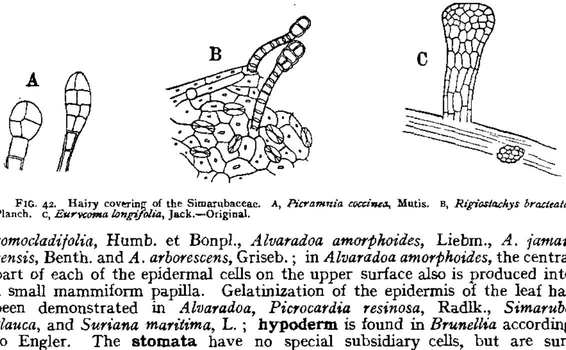

Fig. 42. Hairy covering of the Simarubaceae. A, *Picramnia coccinea*, Mutis. B, *Rigiostachys bracteata*, Planch. C, *Eurycoma longifolia*, Jack.—Original.

comocladifolia, Humb. et Bonpl., *Alvaradoa amorphoides*, Liebm., *A. jamaicensis*, Benth. and *A. arborescens*, Griseb.; in *Alvaradoa amorphoides*, the central part of each of the epidermal cells on the upper surface also is produced into a small mammiform papilla. Gelatinization of the epidermis of the leaf has been demonstrated in *Alvaradoa, Picrocardia resinosa*, Radlk., *Simaruba glauca*, and *Suriana maritima*, L.; **hypoderm** is found in *Brunellia* according to Engler. The **stomata** have no special subsidiary cells, but are surrounded by ordinary epidermal cells; in *Cneoridium dumosum*, Hook. f., and *Balanites aegyptiaca*, Del., stomata are present on both sides of the leaf. Spicular cells are stated by Blenk to occur in the mesophyll in species of *Simaruba, Simaba*, and *Quassia*[1], by Engler in species of *Eurycoma, Hannoa*, and *Mannia*. They are either sclerenchyma-fibres, which run irregularly in the mesophyll (e.g. in *Quassia africana*, Baill., according to my own investigation and in *Eurycoma longifolium*, Jack, according to Engler), or sclerenchyma-cells, which traverse the mesophyll perpendicularly (e.g. in *Simaba cuneata*, according to my own observation) or finally branched sclerenchyma-cells (e.g. in *Simaruba glauca*, according to my own observation, and in *Hannoa Schweinfurthii*, Oliv., according to Engler).

[1] Blenk mentions the following species: *Quassia amara*, L., *Simaba cuneata*, St. Hil., *S. cuspidata*, Spruce, *S. ferruginea*, St. Hil., *S. glabra*, Engl., *S. guianensis*, Aubl., *S. Majana*, Casar., *S. nigrescens*, Engl., *S. suffruticosa*, Engl., *S. trichilioides*, St. Hil.; *Simaruba amara*, Aubl., *S. glauca*, DC., *S. versicolor*, St. Hil.

Oxalate of lime is present in the leaf of *Simaruba glauca* in the form of clustered and solitary crystals; in *Rigiostachys bracteata*, Planch., the cells of the lower epidermis contain one or more small crystals. The secretions occurring in the leaf will be mentioned in the section on the secretory organs of the axis. The **hairy covering** (Fig. 42) consists of clothing and glandular hairs. The former are generally simple unicellular sclerenchymatous trichomes (*Balanites*, *Brunellia*, *Dictyoloma*, *Rigiostachys*); in *Cneorum pulverulentum*, Vent., unicellular two-armed hairs with horizontal arms of equal length occur according to Engler. The ordinary glandular hairs (in species of *Ailanthus*, *Dictyoloma*, *Picramnia*, and *Rigiostachys*) possess a uniseriate stalk of variable length and a spherical or ellipsoidal head, which is divided by horizontal walls only, or by both horizontal and vertical walls, and consists of few or many cells; sometimes the external glands may be club-shaped, when the stalk merges gradually into the head. Glandular shaggy hairs with a multiseriate stalk and a knob-shaped head, which is covered superficially with polygonal cells, are found on the axis of the inflorescence of *Eurycoma longifolium*, Jack.

In connexion with the glandular hairs reference may be made to the curious large glands, visible even to the naked eye, which occur on the auriculiform leaf-teeth of the pinnules of *Ailanthus glandulosa*, Desf., and *A. excelsa*, Roxb.; so far as I know, they have not as yet been examined in detail. They appear to the naked eye as discoid warts, which are slightly depressed in the centre, and are seen to lie on the lower side of the leaf near the termination of the vein running out into the leaf-tooth. In *Ailanthus glandulosa* the chief part of the gland, according to my investigations, consists of a distinctly circumscribed spherical mass of thin-walled cells, which in the dry state are filled with brown contents with scanty secretion, some of them being elongated towards the centre of the external surface of the gland; in the central portion of the gland intercellular spaces elongated in the same direction occur between the cells. Below this mass of cells is a group of terminal tracheides, which represents a branch of the vascular bundle running out into the leaf-tooth. The epidermis of the gland contains no stomata; in surface view it consists of polygonal cells, which are the more elongated radially the nearer they lie to the centre of the external surface of the gland. In the middle of the outer surface the epidermal cells are slightly elongated like a palisade in transverse section, and have a relatively thin external wall. Another very remarkable anatomical feature is of importance in connexion with the function of the gland; the vascular bundle, which passes out into the leaf-tooth, is, in the tooth itself and its neighbourhood, accompanied by a remarkable number of large secretory cells, which especially occupy the entire tip of the tooth. In other parts of the mesophyll of *Ailanthus glandulosa* secretory cells are wanting; they occur, however, in the pith and in the secondary cortex of the axis, as will be described later on.

Concerning the structure of the **rachis** of the leaf and of the **petiole** I abstract the following statements from Casimir de Candolle and Petit. In the species with simple leaves, amongst which *Amaroria soulameoides* and *Samadera indica* have been investigated, the petiole as well as the median vein exhibits an annular closed system of vascular bundles, within which medullary bundles occur; in *Samadera indica* these latter are united to form an inversely orientated ring of wood and bast. In the same way in the species with pinnate leaves[1] which have been investigated, the transverse section of the rachis of the leaf and of the petiole shows an annular closed system of vascular bundles; besides these, in some of the species medullary bundles occur, and their varied orientation can be employed in characterizing species. Medullary bundles have been observed only in species of *Quassia*,

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[1] Species of the genera *Quassia*, *Simaba*, *Simaruba*, *Ailanthus*, *Castela*, *Picrasma*, *Brucea*, *Picraena*, *Picrolemma*, *Dictyoloma*, *Brunellia*, *Picramnia* have been investigated.

Simaba, Simaruba, Ailanthus, Picrasma, and *Picrolemma.* In the species with pinnate leaves a ring of vascular bundles is nearly always present in the median vein of the pinnule; *Picramnia* alone forms an exception among the genera investigated with regard to this point, since in this case the system of bundles has the form of an arc.

3. Structure of the Axis. Concerning the structure of the axis the account given here is based on the statements made in my 'Holzstruktur' and in Möller's 'Rindenanatomie,' as well as on more recent investigations of my own extending to species belonging to twenty-five genera[1].

The transverse section of the **wood** exhibits medullary rays of varied breadth (uniseriate or biseriate in *Quassia amara,* L., as much as 8-seriate in *Ailanthus glandulosa,* rather broad also in *Picraena excelsa,* Lindl.) and vessels with lumina of various sizes (maximum diameter = ·042–·11 mm.). The vessels possess simple perforations almost throughout, and are usually provided with bordered pits on those portions of their walls which abut on wood- or ray-parenchyma. An exception with regard to the perforations is afforded by *Brunellia comocladifolia,* St. Hil., in which, side by side with elliptical elongated perforations, others which are scalariform with few bars are of rare occurrence; an exception with respect to the pitting of the vessel-wall where it is in contact with parenchyma, is presented by the species of *Brunellia* just mentioned, which has large simple pits at these points, and by *Irvingia Barteri,* Hook. fil., which possesses transitions between bordered and large simple pits. The wood-prosenchyma, apart from the tracheides occasionally (*Cneorum tricoccum,* L.) associated with it, has simple pits or such as possess only a narrow border, which is most readily seen in *Koeberlinia spinosa,* Zucc. Delicate division-walls have been observed in the prosenchyma of *Brunellia comocladifolia,* and *Neopringlea integrifolia,* Wats. The wood-prosenchyma may be slightly developed, well marked (*Quassia amara,* L.) or in very considerable abundance, almost forming the groundwork of the wood (*Irvingia Barteri*). The wood-parenchyma is occasionally septate and then contains solitary crystals in the separate cavities (*Simaruba amara,* Aubl., *Irvingia Barteri*).

According to Höhnel, a xylem-mass with tier-like structure occurs in the Jamaica Quassia (*Picraena excelsa,* Lindl.), but not in the Surinam Quassia (*Quassia amara,* L.), and is due to well-marked seriation of the medullary rays and to regular stratiform arrangement of the pits on the libriform elements.

With respect to the **cortex** we may mention that in the majority of the genera the external boundary of the bast is formed by isolated groups of bast-fibres of varied size. Amongst the species investigated by me only a small number are exceptional in this respect, a composite and continuous ring of sclerenchyma being present in this region; these exceptions are—*Ailanthus glandulosa,* Ait., *Alvaradoa arborescens,* Griseb., *A. amorphoides,* Liebm., *Balanites aegyptiaca,* Del., *Brunellia comocladifolia,* St. Hil., *Cadellia pentastylis,* F. v. Müll., *Irvingia Barteri,* Hook. fil., *Koeberlinia spinosa,* Zucc., *Picramnia Antidesma,* Sw., *Quassia amara,* L. The rings of sclerenchyma of *Balanites aegyptiaca* and *Irvingia Barteri* deserve special mention; in the transverse section of the branch of the first-named species the isolated groups of primary bast-fibres become united by a ring of stone-cells situated immediately external to them, not, as elsewhere, by stone-cells placed between

[1] These are: *Quassia, Simaba, Simaruba, Ailanthus, Samadera, Cneorum, Picrasma, Brucea, Picraena, Picrolemma, Eurycoma, Dictyoloma, Cneoridium, Cadellia, Suriana, Brunellia, Irvingia, Harrisonia, Balanites, Spathelia, Picramnia, Picrodendron, Koeberlinia, Alvaradoa, Neopringlea.* The species investigated will be named in the description of the resin-canals (see below).

them; in *Irvingia Barteri* stone-cells thickened on one side (U-shaped) take part in the formation of the ring.

Cork-formation is, so far as is known, superficial. Thus, in *Simaruba excelsa*, DC., *Ailanthus glandulosa*, Ait., *Cadellia pentastylis*, F. v. Müll., and *Alvaradoa*, the cork arises in the outermost cell-layer of the primary cortex; the same is the case in *Brucea ferruginea* (according to Douliot), but not in *Brucea sumatrana*, Roxb., in which the epidermis becomes the phellogen. The periderm is thin-walled in the species of *Ailanthus* and *Simaruba* mentioned, thick-walled in *Cadellia pentastylis*; in *Irvingia Barteri* cork-cells sclerosed on one side only occur.

Concerning the structure of the primary and secondary cortex, the following special statements may be added. In *Balanites aegyptiaca*, Del., and *Koeberlinia spinosa*, Zucc., palisade-tissue is present beneath the epidermis. Groups of stone-cells occur, for example, in the primary cortical parenchyma of *Quassia amara*, L., and *Simaruba versicolor*, St. Hil.; stone-cells thickened on one side only (U-shaped), with the lumen occupied by a crystal, are found in the primary cortex of *Irvingia Barteri* close to the cork-cambium. In the middle of the primary cortex of *Simaba guianensis*, Aubl. var., *Schomburgkiana*, Engl., a continuous ring of stone-cells is developed. The ring of stone-cells in the primary cortex of *Picrolemma Sprucei*, Hook. f., is apparently of the nature of a phelloderm. Stone-cells also occur scattered between the isolated groups of primary bast-fibres, e.g. in *Simaba guianensis*, Aubl. In the secondary bast of many species hard bast-fibres occur, which occasionally differ from the primary bast-fibres in possessing a thinner wall and a wider lumen. I have, for example, met with secondary bast-fibres of this kind in *Simaba guianensis*, Aubl., *Simaruba versicolor*, St. Hil., and *Picraena excelsa*, Lindl.; in *Harrisonia Bennetii*, A. W. Benn. var., and *Neopringlea integrifolia*, Wats., these elements are united by means of stone-cells to form a ring of sclerenchyma, situated in the bast. In *Ailanthus glandulosa*, Ait., groups of stone-cells occur in the secondary bast in addition to the bundles of thick-walled bast-fibres (Möller).

As regards **oxalate of lime**, Möller describes the occurrence of clustered and solitary crystals in the cortex of *Picraena excelsa* and *Ailanthus glandulosa*. Möller's statement, that crystal-sand occurs in *Quassia amara*, L., is incorrect and must be attributed to clustered crystals, which are present, having been broken into fragments in the preparation of the sections. Special crystalline structures are characteristic of the genus *Alvaradoa* only, in which styloids occur in the bast, while clustered and ordinary solitary crystals are alone present in the pith and in the primary cortex of the branches as well as in the tissue of the leaf.

Of **secretory elements**, resin-canals, secretory cells with resinous contents, mucilage-spaces, and secretory cavities with resinous contents are found in the branches.

Resin-canals are not present in all the members of the Order, and are not even constant for a given genus. With the exception of the anomalous genus *Koeberlinia* (comprising the single species *K. spinosa*, Zucc.), which is characterized by resin-canals situated in the bast, these canals occur solely at the margin of the pith, and there is such close connexion with the protoxylem, that they were formerly regarded by Van Tieghem as a component part of the latter. It is further worthy of note that, according to Van Tieghem, the resin-canals are either only situated opposite the interfascicular vascular bundles (*Ailanthus* and *Brucea*), or only opposite the leaf-trace-bundles, which alone possess primary spiral tracheae (*Picraena* and the remainder of the Simarubaceae). The number of the resin-canals varies; their lumen is of varied size, small (e.g. in *Simaruba versicolor* or in *Ailanthus*

glandulosa), or large (e.g. in *Picraena excelsa*). The development of the resin-canals is usually described as schizogenous, but, according to the more recent investigations of Sieck on species of *Ailanthus* and *Brucea* it is schizolysigenous. Leblois met with tyloses in the resin-canals of *Ailanthus glutinosa* and *Brucea ferruginea.*

According to Van Tieghem and my own investigations[1] the secretory canals are found in the following species: **Ailanthus glandulosa*, Ait.; *Amaroria soulameoides*; '*Aruba Cedron*' (=*Simaba Cedron?*); *Brucea ferruginea*, **B. antidysenterica*, Lam., **B. sumatrana*, Roxb.; **Picraena excelsa*, Lindl.; **Picrasma ailanthoides*, Planch.; *Picrocardia resinosa*, Radlk. (according to Radlkofer); **Picrolemma Sprucei*, Hook. f.; **Simaba Cedron*, Planch., **S. cuneata*, St. Hil. et Tul., **S. ferruginea*, St. Hil., **S. glabra*, Engl., **S. Maiana*, Casar., *S. trichilioides*; *Simaruba glauca*, *S. officinalis*, **S. versicolor*, St. Hil.; *Soulamea amara*. On the other hand, the resin-canals are absent in: *Alvaradoa* (according to Radlkofer); **Balanites aegyptiaca*, Del.; **Brunellia comocladifolia*, Humb. et Bonpl., *B. racemiflora*; **Cadellia pentastylis*, F. v. Müll.; *Castela coccinea*; **Cneoridium dumosum*, Hook. f.; **Cneorum tricoccum*, L.; **Dictyoloma incanescens*, DC.; **Eurycoma longifolium*, Jacq.; *Hannoa undulata*; *Harrisonia Brownii*, **H. Bennetii*, A. W. Benn. var.; *Holacantha Emoryi*, Gray (according to Engler); **Irvingia Barteri*, Hook. f., *I. gabonensis*; *Kirkia acuminata*, Oliv. (according to Engler); *Lasiolepis paucijuga*; **Neopringlea integrifolia*, Wats.; **Picramnia Antidesma*, Sw., *P. gracilis*, *P. polyantha*; *Picrella trifoliata*; **Picrodendron juglans*, Griseb.; **Quassia amara*, L.; *Rigiostachys* '*squamata*' (anne sphalm. ex '*bracteata*'?); **Samadera indica*, Gaertn.[2]; **Simaba cuspidata*, Spruce, **S. guianensis*, Aubl., **S. nigrescens*, Engl., **S. suffruticosa*, Engl.; **Spathelia simplex*, L.; **Suriana maritima*, L.

According to Van Tieghem, resin-canals are absent in the root as well as in the entire embryo. On the other hand, in species possessing resin-canals in the peripheral portion of the pith of the branches, they are to be found in similar positions in the petiole, in the median vein of the pinnules, and occasionally even in the lateral veins. In those species in which the resin-canals lie opposite to the leaf-traces in the branches (see above), the systems of resin-canals of branch and leaf are in direct continuity. This is not the case in *Ailanthus* and *Brucea*, in which the resin-canals lie opposite the interfascicular bundles in the branch, so that they do not enter the petiole at the node; consequently the resin-canals of the petiole form an independent system inasmuch as they too are developed secondarily and likewise in connexion with interfascicular bundles.

Secretory cells with resinous contents occur in species either with or without resin-canals: in *Ailanthus glandulosa* in the pith and bast, in *Cneoridium dumosum* and *Harrisonia Bennetii* in the primary cortex and bast, in *Cneorum tricoccum*, *Simaruba versicolor*, *Spathelia simplex*, *Picrella trifoliata* in the pith, bast, and primary cortex. It may be added that these resin-cells are occasionally also present in the tissue of the leaf (in *Cneorum tricoccum*, *Picrella trifoliata*, *Simaruba glauca*, and *Ailanthus glandulosa*, in the last of these species only in the auricles of the pinnules, see above).

Cells with mucilaginous membranes have been met with in the bast and primary cortex of *Picrodendron Juglans*; lysigenous mucilage-spaces in the pith of *Irvingia gabunensis* (according to Van Tieghem), in the pith and primary cortex of *I. Barteri* (according to Pierre and my own observation) and also in the petiole of *Klainedoxa*, Pierre (according to Pierre). Finally it may be mentioned that Blenk has observed secretory cavities in the genera *Cneoridium* and *Spathelia*, and lenticular groups of oil-containing cells which are sharply marked off from the surrounding tissue in the leaf-margin, rachis, and young portions of the stem of *Dictyoloma incanescens*, DC.; these features suggested the advisability of transferring these three genera to the Rutaceae.

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[1] The species the names of which have an * prefixed to them I have investigated myself; the remainder, when not otherwise stated, were investigated by Van Tieghem.

[2] *Contrary to the statements of Van Tieghem!*

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OCHNACEAE.

This Order is distinguished by a series of characteristic anatomical features in the structure of leaf and axis.

The **leaves**[1] are quite glabrous and are devoid of any hairy covering. The type of stoma is characteristic; on either side of the guard-cells a subsidiary cell is placed parallel to the pore. The veins of the leaf are always provided with abundant sclerenchyma. Oxalate of lime occurs only in the form of clustered crystals. The latter are found in association with the sclerenchyma of the veins, and in all the genera and species investigated by me they are there enclosed in cells, the walls of which are of a characteristic structure; thus the cells containing the clustered crystals, which either occur singly or in longitudinal rows above and below the vascular bundles of the veins, are sclerosed on those sides which are directed towards the sclerenchyma of the veins, and also on the adjoining parts of their lateral walls, so that they appear thickened in the form of a U in the transverse section of the leaf; the clustered crystals often appear granulated like crystal-sand[2].

The following remarks may be added regarding the details of the structure of the leaf. The leaf-structure is bifacial, so far as observations extend. The lateral walls of the epidermal cells are either straight (*Luxemburgia*, *Blastemanthus*, &c.) or undulated (*Ochna*). The lateral walls of the epidermal cells of *Ouratea acuminata* are of considerable thickness and are pitted. In *Elvasia calophyllea*, a one-layered continuous hypoderm of elongated fibrous cells with thick walls and narrow lumina, running in the direction of the neighbouring veins, is found below the upper epidermis, the cells of which are four-sided in surface-view. The smaller veins are almost or quite vertically transcurrent. The stomata are present only on the lower surface of the leaf. Sclerenchyma-fibres running irregularly in the inner tissue of the leaf are found in *Cespedesia macrophylla*, *Blastemanthus gemmiflorus*, and *B. grandiflorus*; in *Elvasia calophyllea* branches of the sclerenchyma-fibres accompanying the vascular bundles are sometimes given off from the veins and penetrate the mesophyll.

[1] The following species were investigated by me with regard to their leaf-structure: *Ochna inermis*, Schweinf.; *Ouratea acuminata*, Engl.; *Elvasia calophyllea*, DC.; *Luxemburgia ciliosa*, Gardn.; *Blastemanthus gemmiflorus*, Planch., *B. grandiflorus*, Spruce; *Cespedesia macrophylla*, Seem.

Literature: Gilg, Natürl. Pflanzenfam., iii. Teil, Abt. 6, 1893, pp. 132–4, and Gilg, Anatom. Bau der O. etc., Ber. deutsch. bot. Gesellsch., 1893, pp. 20–5. It may be remarked that besides the genera cited in Durand's Index, Gilg refers the genera *Sauvagesia*, *Leitgebia*, *Lavradia*, *Schuurmansia* and *Neckia* (of the Sauvagesieae) as well as *Lophira* to this Order. (As to the anatomy of the Sauvagesieae see under Violarieae, and regarding the genus *Lophira* see the appendix to the Dipterocarpeae.)

[2] Similar cells with clustered crystals had previously been observed by Vesque (Anat. comp. de l'écorce, Thèse, Paris, 1876, p. 30) in the primary cortex of *Ochna mossambicensis*.

As to the structure of the wood and cortex, the following statements may be made in accordance with my general preliminary investigation of *Ochna arborea*, Burch., *Ouratea vaccinoides*, Engl., and *Luxemburgia speciosa*, St. Hil., and with the statements of Gilg.

As regards the structure of the **wood**[1], in a transverse section of the branch one observes fairly broad medullary rays and vessels with lumina of inconsiderable size (maximum diameter = ·036–·045 mm.); the vessels are either for the most part scattered (*Ochna, Ouratea*), or are radially arranged (*Luxemburgia*). The vessel-walls, where they are in contact with parenchyma of the medullary rays, have bordered pits. The perforations of the vessels are, as a rule, simple and circular or elliptical, but sometimes elongated-elliptical; side by side with these simple perforations, scalariform openings occur in the neighbourhood of the primary wood, and in *Luxemburgia* also in the secondary wood; as a rule they exhibit a small number of bars, and only occasionally in *Luxemburgia* have a larger number. The wood-parenchyma is little developed in *Luxemburgia*, but more abundantly in *Ouratea* and *Ochna*. The wood-prosenchyma, which has thick walls and narrow lumina, shows distinct though not large bordered pits on its walls in *Ochna* and *Ouratea*; in *Luxemburgia* the pits of the prosenchyma are still smaller and occasionally indistinctly bordered. According to Gilg, moreover, the distinctness of the bordered-pitting of the wood-prosenchyma varies very much even within the genus *Ouratea*.

In the **cortex** isolated groups of primary bast-fibres with thick white walls and narrow lumina occur at the outer limit of the bast. The formation of cork is superficial; in *Ochna atropurpurea*, according to Douliot[2], the cork arises in the epidermis; Gilg describes the same place of origin as being quite general, without, however, citing the material investigated. The cork consists of cells with fairly thin walls. In the three species investigated by me the primary cortex is rich in stone-cells. Gilg remarks with respect to the cortex of the Ochnaceae: 'durchweg oft sehr grosse Mengen von Steinzellen.' Typical bast-fibres are wanting in the secondary bast; in their place sclerenchyma-cells with yellow walls, which are elongated in the vertical direction, are more or less like bast-fibres, and abundantly pitted, are present in this tissue in the three species examined by me.

According to Gilg, the occurrence of cortical vascular bundles, which are met with in every species, is very characteristic of the Order. They are leaf-trace-strands, which, previous to bending out towards the leaf, run for long distances in the cortex, during which they sometimes divide several times. According to Gilg, medullary bundles also frequently occur, e.g. in the genus *Godoya* in large numbers.

I have not observed special secretory elements, the presence of which one might be led to infer from the statements of authors[3]—'arbores, succo aqueo.' Gilg likewise only mentions that the cortex, pith, and medullary rays in this Order often contain large quantities of tannin, so that these parts of the dried plants appear of a deep dark-red colour.

Appendix: On the genus *Tetramerista*.

The genus *Tetramerista* with the species *T. glabra*, Miq., which hitherto has always been referred to the Ochnaceae, must, according to Gilg's investigations (loc. cit.), certainly be excluded from this Order. Gilg has not yet found a definite relationship for *Tetramerista*, as the floral material available is insufficient. However, according to Gilg, *Tetramerista* shows most points of agreement with the Theaceae.

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[1] Solereder, 'Holzstruktur,' 1885, p. 94.
[2] Douliot, Ann. sc. nat., sér. 7, t. x, 1889, p. 342.
[3] Endlicher, Gen. Plant., p. 1141, Bentham and Hooker, Gen. Plant., i, p. 316, etc.

On the anatomical side the lack of cortical bundles favours the separation of the genus *Tetramerista* from the Ochnaceae. The occurrence of raphide-sacs in *Tetramerista* is, further, not unfavourable to the view of a relationship with the Ternstroemiaceae, for, although the Theaceae do not possess raphides, yet the Saurauieae and Marcgravieae do.

BURSERACEAE.

1. Review of the Anatomical Features. The Burseraceae[1] are characterized in an excellent manner by the possession of resin-canals in the bast (cf. Fig. 44), by the occurrence of a composite and continuous ring of sclerenchyma in the cortex, by the presence of large simple pits on the vessel-wall where it is in contact with parenchymatous cells, by the occurrence of exclusively simple perforations in the vessels, of narrow medullary rays, and of simply-pitted, sometimes septate wood-prosenchyma-cells, and lastly by the lack of a special type of stoma.

The formation of cork is superficial. Oxalate of lime is present in the form of clustered or solitary crystals. The internal secretory system, apart from the balsam-canals in the phloem, consists of resin-canals, which are situated in the pith (species of *Boswellia* and *Protium*) or in the primary cortex (species of *Canarium*), and of mucilaginous cells, or of groups of such cells, which occur in the primary cortex (species of *Hedwigia* and of (?) *Garuga* and *Protium*) or in the mesophyll (species of *Protium*). Gelatinization of the epidermis of the leaf is of widespread occurrence. The hairy covering (Fig. 43) consists of clothing and glandular hairs. Special forms of the clothing hairs are:—unicellular two-armed hairs (*Protium*), unicellular hooked hairs (*Garuga*), and peculiar tufted hairs (*Santiria*); the glandular hairs exhibit numerous forms. The following are additional special features deserving mention in the structure of the leaf and axis respectively: the occurrence of hypoderm on the upper side of the leaf (*Dacryodes hexandra*, Griseb.); the papillose differentiation of the lower epidermis of the leaf (*Protium Riedelianum*, Engl.); the occurrence in the species of *Canarium* (excl. *Scutinanthe*) of medullary vascular bundles, which are inversely orientated with regard to the position of xylem and phloem.

2. Structure of the Leaf. A thorough investigation of the leaf-structure of the Burseraceae is still wanting. Gelatinization of the **epidermis** of the leaf has been observed in very many members of the Order[2]. According to Radlkofer, *Protium Riedelianum*, Engl., has papilla-formation on the lower side of the leaf; *Dacryodes hexandra*, Griseb., has a 1–2-layered hypoderm on the upper side. The stomata, in the more fully investigated species, are found only on the lower side of the leaf, and each of them is surrounded by several ordinary epidermal cells. The stomata of *Santiria mollis*, Engl. (Fig. 43, *A–B*), which have a widely open pore and occur on the tips of columnar elevations

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[1] It should be mentioned at this point that the genus *Paivaeusa*, Welw., which in Durand's Index is still included in the Burseraceae, has been removed by Radlkofer (Glied. d. Sapindac., Sitz.-Ber. Münch. Akad., 1890, p. 341) to the Euphorbiaceae, being placed in the immediate neighbourhood of the genus *Oldfieldia* among the Phyllantheae; anatomical features gave the primary grounds for this transference (viz. the absence of the composite and continuous sclerenchyma-ring, and its replacement by isolated groups of primary bast-fibres developed in the radial direction; the lack of balsam-canals and the presence of a peculiar hairy covering, consisting of two-celled trichomes; and lastly the occurrence of two subsidiary cells parallel to the guard-cells). It may likewise be mentioned that the Burseraceous genus *Ganophyllum* which is mentioned by Engler in his monograph, and which has no balsam-canals in its phloem, has been transferred by Radlkofer (*Cupania*, in Sitz.-Ber. Münch. Akad., 1879, p. 591) to the Sapindaceae.

[2] Namely: *Garuga pinnata*, Roxb.; *Commiphora caudata*, Engl.; *Boswellia serrata*, Roxb. and *B. pubescens*, Engl.; *Bursera gummifera*, Jacq.; *Crepidospermum rhoifolium*, Tr. et Pl.; as well as numerous species, cited by Blenk, belonging to the genera *Commiphora*, *Protium*, *Bursera*, *Canarium*, and *Hedwigia*.

above the network of the veins, are extremely peculiar. The leaf-structure is bifacial in *Protium unifoliolatum*, Engl., and in *Dacryodes hexandra*, Griseb. *Protium unifoliolatum* and *P. Spruceanum*, Engl., have vertically transcurrent veins.

Oxalate of lime is contained in the leaf in the form of clustered and ordinary solitary crystals. *Garuga pinnata* and *Boswellia serrata*, for example, possess clustered crystals both in the mesophyll and in the veins; *Protium unifoliolatum*, *Hedwigia balsamifera*, and *Dacryodes hexandra* have solitary crystals. Well-developed large solitary crystals in the palisade-tissue give rise to clear transparent dots in *Protium javanicum*, Burm., and *P. serratum*, Engl. Silicified groups of cells have been demonstrated in the lower epidermis of the leaf of *Protium Spruceanum*.

Regarding the occurrence of internal **secretory organs** in the leaf it may be mentioned, in the first place, that the balsam-canals, which will be discussed more fully under the structure of the branch, are met with in the phloem of

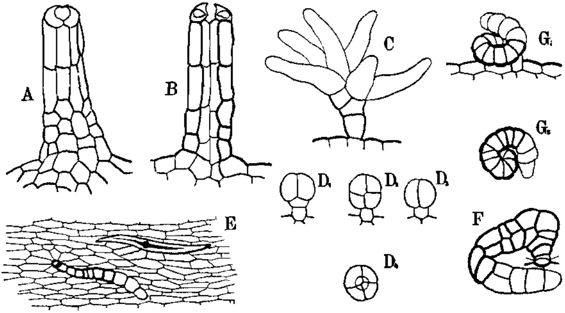

FIG. 43. A–B, Elevated stomata of *Santiria mollis*, Engl. C, Branched trichome ot *Santiria mollis*. D–G, External glands: D, *Boswellia papyrifera*, Hochst.; E, *Protium Spruceanum*, Engl.; F, *Canarium hispidum*, Bl.; G, *Crepidospermum rhoifolium*, Tr. et Planch.—Original.

the larger veins. A peculiar feature, which may be appended here, has been demonstrated by Blenk in members of the genera *Canarium*, *Trattinickia*, and *Santiria*, namely, the local appearance of palisade-cells with little or no chlorophyll, and often having somewhat mucilaginous walls; they frequently cause the formation of a rent in the mesophyll on drying the leaf. The same author mentions the occurrence of cells in the mesophyll of *Protium unifoliolatum*, Engl., and *P. pubescens*, Engl., which have clear contents like water, and, according to my own investigation of *P. unifoliolatum*, have proved to be cells with mucilaginous walls.

The **hairy covering** is formed by clothing and glandular hairs. The commonest form of clothing hair is represented by simple unicellular, often sclerenchymatous, trichomes (*Garuga pinnata*, &c.). Moreover, in *Garuga pinnata*, unicellular hooked hairs are found, in *Protium Spruceanum* short unicellular two-armed hairs, with thick walls and arms of equal length (Fig. 43, *E*), and in the genus *Zanha*, Hiern, which is provisionally referred to the Burseraceae, peltate hairs, the structure of which has not yet been examined. It is still

undecided whether the peculiar tufted hairs of *Santiria mollis* (Fig. 43, *C*), which are composed of a short, uniseriate and thick-walled stalk and of a tuft of tubular terminal cells with thin walls and brown contents, must be included among the glandular hairs. The form of the glandular hairs is manifold. The external glands of *Boswellia papyrifera*, Hochst. (Fig. 43, *D*), have a short 1–2-celled stalk and a spherical head, which is 2–4-celled owing to division in different directions. *Garuga pinnata* and *Canarium acutum*, Engl., have similar glandular hairs which, however, have longer stalks. External glands, which are filiform, uniseriate, and slightly broadened towards their tips, characterize *Protium Spruceanum* (Fig. 43, *E*). Finally, peculiar external glands (which are tubular and curved or rolled up like a snail, devoid of a stalk, and consisting essentially of one row of cells only doubled in places) are found in *Canarium hispidum*, Bl. (Fig. 43, *F*), *Crepidospermum rhoifolium* (Fig. 43, *G*), *Dacryodes hexandra*, *Santiria mollis*, and *S. bornensis*, Engl.

As to the structure of the **rachis**[1] the following points from C. de Candolle's treatise may be mentioned. It shows in transverse section a closed ring of vascular bundles. Medullary bundles are found only in species of *Icicopsis*, *Canarium*, and *Trattinickia*; in *Icicopsis brasiliensis* they are united into a bundle-ring, which is inversely orientated with respect to the position of wood and bast; in *Canarium tomentosum*, on the other hand, they are separate and arranged in two concentric circles.

3. Structure of the Axis. The following description is based on the statements in the literature as well as on my own casual examination of the species enumerated below[2].

The occurrence of a composite and continuous ring of sclerenchyma[3] in the pericycle is primarily characteristic for the axis of the Burseraceae. In herbarium branches it consists of arcs of bast-fibres, which are convex on their outer sides, and of stone-cells situated between them. In thicker branches the undulated course of the sclerenchyma-ring shows up less distinctly, because the arcs of bast-fibres are broken up into smaller bundles, and the latter are united by groups of stone-cells.

A second, equally valuable character of the axis in the Burseraceae is the occurrence of **resin-canals** in the bast, which Engler was the first to set up as an important character for the delimitation of the Order. These resin-canals have been demonstrated in all the genera enumerated in Durand's Index (with the exception of *Paivaeusa*, regarding which, see note 2, p. 215) as well as in the genus *Aucoumea*, newly instituted by Pierre. All these genera have one large resin-canal immediately within each pericyclic arc of hard bast, and, besides these, resin-canals with small lumina in the secondary bast. In certain species medullary balsam-canals have also been observed (*Boswellia papyrifera*, Hochst., *B. serrata*, Roxb., *Canarium microcarpum*, Engl., and *Protium serratum*, Engl.), as well as short resin-canals running in the primary cortex (in *Canarium australasicum*, F. v. Müll., *C. decumanum*, Gaertn., and *C. zeylanicum*, Bl., but not in all the species of this genus, and, further, in *Bursera Delpechiana*, Poiss., according to J. Möller). The origin of the resin-canals is schizolysigenous (Sieck[4]).

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[1] Species of *Garuga*, *Protium*, *Bursera*, *Icicopsis*, *Canarium*, *Crepidospermum*, *Trattinickia*, and *Hedwigia* have been investigated.

[2] These are: *Garuga pinnata*, Roxb.; *Commiphora caudata*, Engl.; *Boswellia serrata*, Roxb., *B. pubescens*, Engl.; *Bursera gummifera*, Jacq.; *Protium unifoliolatum*, Engl.; *Crepidospermum rhoifolium*, Tr. et Pl.; *Hedwigia balsamifera*, Sw.; *Trattinickia burseraefolia*, Mart.; *Canarium acutum*, Engl.; *Dacryodes hexandra*, Griseb.; *Santiria glabrifolia*, Engl.

[3] The figures given by Marchand and Engler, which represent the sclerenchyma-rings of *Commiphora africana*, Engl., *Protium obtusifolium*, March., and *Bursera leptophloeos*, Mart., respectively as interrupted, are inexact; as also are Jadin's figures representing the same feature.

[4] According to J. Möller (loc. cit.) the seat of the Mexican linaloe-oil produced by some species

The following statements may be made with regard to the structure of the **wood.** The medullary rays are always narrow. The diameter of the vessels attains a maximum of ·045–·126 mm. The vessels have simple perforations throughout. In contact with one another the walls of the vessels bear densely packed, large bordered pits (diameter of the border = at least ·004 mm.), but in contact with ray-parenchyma they bear large simple pits with transitions to bordered pits. The large simple pits, groups of which frequently recall a scalariform perforation of a vessel, form a third excellent character of the axis in the Burseraceae. The groundwork of the wood is formed by wood-prosenchyma with simple pits and lumina, which are usually

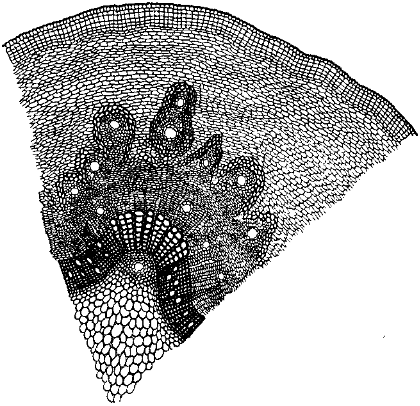

FIG. 44. Transverse section through a young axis of *Boswellia serrata*, Roxb.—Original.

wide and never very narrow, while in all the species investigated they are now and then provided with delicate division-walls. The wood-parenchyma is usually little developed, but is more abundant, e. g., in *Boswellia papyrifera*, Hochst.

Regarding the structure of the **cortex** the following may be added to what has been said above. The origin of the cork, which has been investigated by Jadin in all the genera except *Triomma*, is always superficial; it is usually subepidermal, rarely (*Santiria*) somewhat deeper, arising in the outer layers of the primary cortex. It is worthy of note that in many members of the Order, especially species of *Boswellia* and *Commiphora*, even in branches which are only as thick as one's finger, layers of cork peel off like a skin every year, and can be used as paper. Stone-cells are present in the primary cortex in all the species of *Protium, Trattinickia, Canarium, Dacryodes*, and *Santiria* I have

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of *Bursera* is not the resin-canals discussed above, but (in *B. Delpechiana*, Poir.) the cells of the wood, in which the oil does not appear as a secretion but as an ordinary component of the contents, while in *B. Aloexylon*, Engl., it is also found in special large thin-walled oil-cells in the wood.

examined; sclerosed parenchyma with wide lumina is found in the same region in *Garuga pinnata* (here it is occasionally somewhat branched) and in *Bursera gummifera*. I have met with groups of bast-fibres, sometimes in the form of bands, in the secondary bast in the above-named species of *Garuga*, *Trattinickia*, *Canarium*, and *Santiria*.

Apart from the balsam-canals already discussed, secretory elements of a different nature occur in certain species; these elements are situated in the primary cortex and will most probably all prove to be cells with mucilaginous membranes or mucilage-spaces derived from groups of such cells.

I was able at least to show that this was the case in *Hedwigia balsamifera*, in which Jadin describes the occurrence of 'cavités sécrétrices plus ou moins allongées dans l'écorce.' The remaining cases, which should probably be classed here, still require further examination. They are: the lysigenous secretory spaces observed by Engler in the primary cortex of *Protium Blanchetii*, Engl., which Marchand, to judge from his drawing, appears to have seen also in *Protium obtusifolium*, March.; and the 'glandes sécrétrices corticales' demonstrated by Jadin in the same position in the genus *Garuga*.

Lastly, the occurrence of **medullary vascular bundles** in the genus *Canarium* must be mentioned (Radlkofer, Jadin). They are arranged in a circle and are inversely orientated with regard to their xylem and phloem; the phloem-groups are turned towards the centre of the pith, and contain one large balsam-canal each, like the bundles of the normal ring. It should be noted that the medullary bundles are sometimes (*Canarium acutum*) rudimentary, being reduced to a bundle of prosenchyma enclosing a large resin-canal. Jadin has demonstrated the medullary vascular bundles in question in twenty-seven species. They are only wanting in *Canarium brunneum*, Raddi (*Scutinanthe brunneum*, Thw.), which is Jadin's reason for again instituting the genus *Scutinanthe*.

Literature: Marchand, Adansonia, t. vii, *1866–7*, p. *258* and pl. viii, and t. viii, *1867–8*, pp. 56 and 74 et seq. and pl. ii, iii.—Engler, Verw.-Verh. der Rutaceae etc., Halle a. S., 1874.—Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 98, 99, and 394.—De Bary, Vergl. Anat., 1877.—Cas. de Candolle, Anat. comp. d. f., Mém. Soc. phys. et nat. de Genève, t. xxvi, 2, 1879, pp. 439 and 463, pl. i.—Möller, Rindenanat., 1882, pp. 321, 322.—Engler, Suites au Prodr., vol. iv, 1883, p. 2.—Radlkofer, Abh. naturw. Ver. Bremen, Bd. viii, 1883, p. 429 note.—Blenk, Flora 1884, p. 296 et seq., separate copy, pp. 55–8.—Solereder, Holzstr., 1885, pp. 94, 95.—Radlkofer, Sitz.-Ber. Münch. Akad. *1886*, p. *307*.—Radlkofer, Glied. d. Sapindac., Sitz.-Ber. Münch. Akad. *1890*.—Jadin, Journ. de Bot. 1893.—Jadin, Contribut. à l'étude des Térébinthacées, Montpellier, 1894.—Jadin, Ann. sc. nat., sér. 7, t. xix, 1894, pp. 1 and 48 et seq.—Baur, Burs. Opoponax, Diss., Bern, 1894, pp. 39 et seq.—Sieck, Sekretbeh., Diss., Bern, 1895.—Engler, in Natürl. Pflanzenfam., iii. Teil, Abt. 4, 1896, pp. 230, 231.—Pierre, Bull. Soc. Linn. Paris, 1896, p. 1240.—J. Möller, Lignum Aloes, Pharm. Post, 1897.

MELIACEAE.

1. Review of the Anatomical Features. This Order is characterized anatomically: by the occurrence of secretory cells, which are met with almost throughout in the leaf-tissue, where they frequently give rise to transparent dots, and sometimes also in the pith and cortex of the axes; by the lack of special subsidiary cells adjoining the stomata; by the simple perforations of the vessels; by the wood-prosenchyma, which has simple pits and, in most cases, has fairly wide lumina which are often septate; by the differentiation of bordered pits even on the parts of the vessel-walls which adjoin parenchyma; and, lastly, by the superficial origin of the cork and by the isolated groups of bast-fibres in the pericycle.

The secretory cells are absent from the leaf in the genera *Chloroxylon* and *Flindersia*, but are present in the cortical tissue of the axis. Moreover, these two genera are further characterized by the occurrence of secretory cavities in

the tissue of the leaf and cortex, and it is therefore better to remove them to the Rutaceae as has been done by Engler.

Oxalate of lime occurs in the form of ordinary solitary and clustered crystals. The hairy covering (Fig. 45) consists of simple unicellular or uniseriate hairs, of unicellular two-armed hairs (*Amoora, Dysoxylum*) or of transitional forms between simple and two-armed hairs (*Chisocheton, Dasycoleum, Sandoricum*), of stellate (*Aglaia, Melia, Pterorhachis*) and peltate hairs (*Aglaia, Amoora, Flindersia*), and, lastly, of glandular hairs of different forms, which in *Cabralea* are sunk in very deep pits in the leaf.

Finally, the following are special characters for the diagnosis of genera and species : gelatinization of the epidermis of the leaf (*Chukrasia* and Cedreleae) ; hypoderm on the upper side of the leaf (*Carapa moluccensis*, Lam.) ; papillose differentiation of the epidermal cells on the lower side of the leaf (species of *Ekebergia* and *Walsura*) ; spicular cells in the mesophyll (species of *Dysoxylum*) ; crystal-idioblasts in the mesophyll (species of *Aglaia, Dysoxylum, Meliadelpha*) ; occurrence of secondary hard bast ; occurrence of stone-cells, groups of stone-cells or rings of stone-cells in the primary cortex ; and, lastly, the varied form of the secretory cells, which are either rounded and isodiametric or elongated to a varying extent (in the latter case the secretory cells sometimes forming longitudinal rows), and either unbranched or branched.

2. Structure of the Leaf. Our knowledge of the leaf-structure is essentially based on the statements of Blenk, and requires further investigation. The following points may be mentioned regarding it.

In the species examined by me (*Melia Azedarach*, L., *Swietenia Mahagoni*, L., *Trichilia Claussenii*, C. DC., *Cedrela Toona*, Roxb., *Aitonia capensis*, Thunb., and *Ptaeroxylon utile*, Eckl. et Zeyh.) the stomata are restricted to the lower surface of the leaf, and each is surrounded by several ordinary epidermal cells. Mucilaginous **epidermal cells** have been observed by Blenk in *Chukrasia tabularis*, A. Juss., where they give rise to transparent dots, and in the Cedreleae ; formation of epidermal papillae has been observed in *Ekebergia Rueppeliana*, A. Rich., *Walsura hypoleuca*, Kurz, *W. Piscidia*, Roxb., *W. tabulata*, Hiern, &c. (Radlkofer) ; a two-layered hypoderm below the small-celled epidermis of the upper side of the leaf, the lower layer being considerably elongated like palisade-tissue, is found in *Carapa moluccensis*, Lam. (Schimper) ; and, lastly, spicular cells, thick-walled, simple or branched sclerenchymatous cells, which traverse the mesophyll like buttresses, occur in *Dysoxylum acutangulum*, Miq., *D. cyrtobotryum*, Miq., and *D. macrocarpum*, Bl. (Blenk and Radlkofer).

The characteristic feature of the leaves of the Meliaceae is the **secretory cells,** which, however, also occur in the axis (viz. in the bast and primary cortex) and very frequently cause transparent dots. They are found not only in the members of the Melieae, Trichilieae, and Swietenieae, as Blenk has shown, but also in the genera of Cedreleae—*Cedrela, Chloroxylon*, and *Flindersia*, in the two genera last named, however, only in the branch (secondary bast), and not in the leaf. The form of the secretory cells in question varies. They are either spherical or ellipsoid with a diameter of ·01–·03 mm., or they are tubular and elongated parallel to the surface of the leaf, and in that case may attain a length of 3 mm. and more (up to 1 cm. in *Cabralea*). Frequently the secretory cells branch, sending out either short or fairly long protrusions parallel to the surface of the leaf. In some cases, in place of a long branched or unbranched tubular secretory cell, one finds a row of secretory cells lying one behind another, and as an extreme case these rows of secretory cells are sometimes branched. The secretory cells are ordinarily found at the boundary of palisade and spongy parenchyma, more rarely in one or the other of these tissues. In rare cases (*Megaphyllaea*) they are restricted to the neighbourhood of the vascular bundles.

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A synopsis of the genera in which Blenk has demonstrated secretory cells in the leaf follows, arranged in the serial order of Durand's Index; the form and arrangement of the secretory cells are represented thus: r=rounded, l=rather long, ll=long, b=branched, R=in rows. Tribe 1, Melieae: *Cipadessa* r, *Quivisia* r, *Turraea* l b, *Naregamia* l, *Munronia* l, *Melia* r, *Azadirachta* r l. Tribe 2, Trichilieae: *Sandoricum* r, *Cabralea* ll, *Dysoxylum* r b l ll R, *Chisocheton* r l, *Dasycoleum* ll, *Guarea* R r l, *Amoora* r l b R, *Synoum* l, *Aglaia* r l ll b R, *Hearnia*, *Walsura* r ll, *Ekebergia* r, *Trichilia* r l b R, *Heynea* r. Tribe 3, Swietenieae: *Carapa* r, *Khaya*, *Soymida* r, *Swietenia* r, *Chukrasia* r. The secretory cells, moreover, as may be added here, also occur in the genus *Meliadelpha* founded by Radlkofer (and previously=*Paullinia oceanica*, Bull), in *Megaphyllaea* as well as in the genera *Aitonia* and *Ptaeroxylon*, transferred by Radlkofer to the Meliaceae, and in the Cedreleae (regarding the latter, see above). With regard to the varied form, &c., of the secretory cells, according to Blenk, the members of the smaller genera as a rule appear to agree, and so do, at any rate, small groups of allied species in the larger genera.

In addition to the secretory cells in two genera of Cedreleae, *Chloroxylon*, and *Flindersia*, secretory cavities occur, which are to be found not only in the leaf-tissue, but also in the primary cortex of the branches.

Oxalate of lime is excreted in both leaf and axis only in the form of ordinary solitary and clustered crystals. The occurrence of solitary crystals (*Cabralea*, *Dysoxylum*, *Chisocheton*, *Dasycoleum*, *Guarea*, *Amoora*, *Synoum*, *Aglaia*, *Hearnia*, *Cedrela*, *Meliadelpha*) or of clustered crystals (Melieae, *Trichilia*, *Heynea*) in the palisade-tissue is, according to Blenk's statements, of value in detailed classification. The solitary crystals present in the palisade-tissue sometimes (*Aglaia*), when of sufficient size, appear as transparent dots.

The **hairy covering** consists of clothing and glandular hairs. Of clothing hairs one finds firstly simple unicellular (*Aitonia*, *Ptaeroxylon*) or uniseriate (*Cedrela*) trichomes. Unicellular two-armed hairs have been observed by Radlkofer on the leaf of *Dysoxylum ptychocarpum*, Radlk., and, at any rate, on parts of the flower or fruit in other species of *Dysoxylum* and in *Amoora Balanseana*. In other members of the Order a tendency to the formation of Malpighian hairs is indicated by the fact that the simple trichomes, which are adpressed to the organs bearing them, show a pocket-like expansion of the basal part of the hair close above its point of insertion (parts of the flower and fruit of species of the genera *Chisocheton*, *Dasycoleum*, and *Sandoricum* according to Radlkofer). Further, stellate hairs occur (in *Melia* and *Aglaia* according to Bentham and Hooker's 'Gen. Plant.,' and in *Pterorhachis* according to Harms, in Engler's 'Bot. Jahrb.' 1895), and also peltate scales (in *Aglaia*, *Amoora* and *Flindersia*). According to O. Bachmann the peltate hairs of *Aglaia* and *Amoora* recall the peltate scales of the Sterculiaceous genus *Heritiera* in the arrangement of their cells; they are sunk in small pits in the strongly cuticularized leaf-surface. Moreover, in *Aglaia Roxburghiana*, Bedd. several simple ray-cells project from the middle of the shield, and in *A. argentea*, Bl. still another type of scale occurs, namely a long-stalked peltate hair, the ray-cells of which have thin walls and form a conical elevation in the middle of the shield. The peltate hairs of *Flindersia* are represented in Fig. 45, *B*. The glandular hairs, which are always multicellular, have been observed (*a*) in species of *Cedrela* (Fig. 45, *A*), in which they have a club-shaped form, but are sometimes differentiated into a uniseriate stalk and a multicellular head; (*b*) in *Ptaeroxylon* and *Flindersia*, where they have a more spherical or an inversely conical glandular head; and (*c*) in *Cabralea*, where they are sunk in deep pits sometimes reaching as far as the middle of the leaf, and can be recognized even with a lens as dots of the size of a pin-prick.

The **petiole**, or the rachis as the case may be, has been much more fully investigated than the lamina, namely by C. de Candolle in 138 species repre-

senting nearly all the genera[1]. This investigation has given the following results. The species with simple leaves (i. e. all the species of *Quivisia* and *Turraea* as well as certain species of *Walsura* and *Trichilia*) show an arc of vascular bundles in the transverse section of the petiole and of the midrib of the leaf. On the other hand, in the species with pinnate leaves, the rachis of the leaf and the midrib of the pinnules possess a ring of vascular bundles as seen in transverse section. Cortical vascular bundles do not occur in any case in the petiole or in the rachis, and medullary bundles are found only in twelve species of the genera *Walsura*, *Vavaea*, *Trichilia*, *Soymida*, and *Heynea*.

3. Structure of the Axis. In the following account, besides the literature, an unpublished investigation of my own, which extended to the species cited in the list below[2], has been made use of.

In transverse section the **wood** exhibits narrow medullary rays, as much as three cells in breadth, and vessels with lumina of different sizes (maximum diameter = ·036–·11 mm.). The vessel-wall, where it is in contact with parenchyma, always bears bordered pits only. The narrower vessels of *Melia Azedarach* possess spiral thickening. The perforations of the vessels are simple throughout. The wood-parenchyma may either be little developed

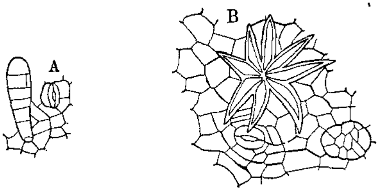

Fig. 45. A, Lower epidermis of the leaf of *Cedrela Toona*, Roxb. with a glandular hair. B, Lower epidermis of the leaf of *Flindersia maculata*, F. v. Müll. with a peltate and a glandular hair.—Original.

or rather abundant (*Melia*, *Swietenia*, *Trichilia*, *Megaphyllaea*). The wood-prosenchyma has simple pits and in many species (of the genera *Cabralea*, *Cipadessa*, *Amoora*, *Dysoxylum*, *Soymida*, *Chisocheton*, *Carapa*, *Guarea*, *Vavaea*) it is septate. Wood-prosenchyma with narrow lumina is rare (*Elutheria microphylla*, *Azadirachta indica*). Lastly, in *Carapa guianensis*, Aubl., resin-cavities arise in the wood by disorganization of groups of cells (Möller); in *Swietenia Mahagoni*, L., *Guarea trichilioides*, L., and *Chloroxylon Swietenia*, DC., a tier-like construction of the wood has been shown to occur (Höhnel).

The development of the cork takes place subepidermally (*Melia*, *Trichilia*, *Guarea*, *Cedrela*, according to Möller). The cork-cells have thin or somewhat

[1] *Turraeanthus*, *Naregamia*, *Philastrea*, *Pseudocarapa*, *Owenia*, *Lansium* and *Beddomea* have not been investigated.

[2] *Cipadessa baccifera*, Miq., *Quivisia oppositifolia*, Cav., *Turraea abyssinica*, Hochst., *Naregamia alata*, W. et A., *Munronia Wallichii*, Wight, *Melia Toosendan*, Sieb. et Zucc., *Azadirachta indica*, A. Juss.; *Sandoricum indicum*, Cav., *Cabralea Cangerana*, Sald., *Didymocheton Leschenaultianum*, Juss., *Chisocheton divergens*, Bl., *Megaphyllaea perakensis*, Hemsl. (Herb. Kew), *Dasycoleum Philippinum*, Turcz., *Guarea humilis*, Bert., *Amoora Rohituka*, W. et A., *A. Lawi*, Benth. et Hook., *Synoum glandulosum*, Juss., *Aglaia paniculata*, Kurz, *Hearnia sapindina*, F. v. Müll., *Walsura piscidia*, Roxb., *Ekebergia Rueppeliana*, Rich., *Vavaea amicorum*, Benth., *Trichilia Weddelii*, C. DC., *T. paraensis*, C. DC., *Heynea trijuga*, Roxb.; *Carapa moluccensis*, Lam., *Soymida febrifuga*, A. Juss., *Swietenia humilis*, Zucc., *Elutheria microphylla*, C. DC., *Chukrasia tabularis*, A. Juss.; *Cedrela Toona*, Roxb., *Chloroxylon Swietenia*, DC., *Flindersia maculata*, F. v. Müll.; *Aitonia capensis*, Thunb., *Ptaeroxylon utile*, Eckl. et Zeyh.

thickened walls. In almost all the members of the Order isolated groups of bast-fibres are found in the pericycle. The only exceptions are afforded by *Cabralea Cangerana*, in which an interrupted composite sclerenchyma-ring is present in the pericycle, and by *Flindersia maculata*, where sclerenchyma is quite wanting in the pericycle. In most cases[1] the secondary bast likewise contains hard bast, which is developed in the form of scattered fibres, or small groups, bands or rings of bast-fibres. In a similar manner the primary **cortex** either contains ordinary solitary stone-cells (*Vavaea amicorum*, *Amoora Rohituka*, *Hearnia sapindina*), or groups of stone-cells (*Cabralea Cangerana*, *Dasycoleum Philippinum*, *Synoum glandulosum*, *Chisocheton divergens*, *Megaphyllaea perakensis*), or slightly sclerosed parenchyma (*Trichilia Weddelii*, *Guarea humilis*), or branched stone-cells (*Aglaia paniculata*), or lastly a ring of stone-cells (*Sandoricum indicum*, *Amoora Lawi*, *Didymocheton Leschenaultianum*).

Finally, it may be mentioned with respect to the **pith** that groups of stone-cells sometimes (*Cabralea Cangerana*, *Hearnia sapindina*, *Didymocheton Leschenaultianum*) also occur in this tissue; or groups of prosenchymatous cells are found, e. g. in *Sandoricum indicum*, *Chisocheton divergens*, and *Megaphyllaea perakensis*.

Literature: Vesque, App. lact. de l'*Hartigsea*, etc., Bull. Soc. bot. de France 1873, pp. 232–5.—Engler, Verw.-Verh. d. Rutac. etc., Halle a. S., 1874, p. 40.—Moller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 84–7 and 380.—C. de Candolle, in Flor. brasil., vol. xi, 1, 1878, p. 166 and Taf. 51, ii, in Suit. au Prodr., t. i, 1878, p. 404 and Mém. Soc. phys. et nat. de Genève, t. xxvi, 2, 1879, pp. 435 and 455 et seq. and pl. i.—Radlkofer, *Cupania*, Sitz.-Ber. Münch. Akad. 1879, p. 593 et seq.—Möller, Rindenanat., 1882, pp. 259–65.—Höhnel, Sitz.-Ber. Wiener Akad., Bd. lxxxix, Abt. 1, 1884, p. 39.—Blenk, Flora 1884, p. 339 et seq., separate copy, pp. 58–68.—Solereder, Holzstr., 1885, p. 95.—O. Bachmann, Flora 1886, separate copy, p. 35.—Solereder, Vergl. Anat. der Aristolochiac., Engler, Bot. Jahrb., Bd. x, 1888, p. 411.—Radlkofer, Glied. d. Sapindac., Sitz.-Ber. Münch. Akad. 1890.—Schimper, Indomalayan. Strandfl., Jena, 1891, p. 16 and Taf. iv.—Harms, in Natürl. Pflanzenfam., 3. Teil, Abt. 4, 1896, pp. 260–1.

CHAILLETIACEAE (DICHAPETALEAE).

This Order is distinguished by a series of anatomical characters. Among these are: the stomata, which have subsidiary cells parallel to the pore, and occur only on the lower side of the leaf; the superficial origin of the cork; the pericycle with isolated groups of primary bast-fibres; the usually simple and only sporadically scalariform perforations of the vessels; the bordered pitting of the wood-prosenchyma (according to Barth); the hairy covering, formed solely by simple unicellular hairs (Fig. 46) which are characterized by small conical or wart-shaped excrescences on their cell-walls, while glandular hairs are absent. Oxalate of lime is deposited in the form of clustered and ordinary solitary crystals. Of secretory elements we may mention: cells with mucilaginous walls in the epidermis of the leaf, in the hypoderm, and in the ground-tissue of the petiole and branch in certain members of the Order, as well as large secretory cells with brown contents, which occur in the mesophyll of *Chailletia Dichapetalum*,

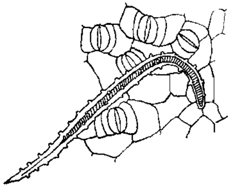

FIG. 46. Lower epidermis of the leaf of *Tapura amazonica*, Poepp. et Endl.—Original.

[1] Except the species cited of *Naregamia*, *Heynea*, *Vavaea*, *Elutheria*, *Soymida*, *Hearnia*, *Chloroxylon* and *Flindersia*.

R. Br., and are either shaped like palisade-cells or are spherical to ellipsoid in form.

In amplification of the preceding anatomical diagnosis, the following facts may be added in accordance with Barth's work[1] and my own observations[2]. The **leaf-structure** is mostly bifacial. The palisade-tissue usually consists of short cells and is not very typical; the spongy parenchyma is sometimes wanting (*Chailletia cymosa*, Hook., according to Barth). According to Barth, the occurrence of sclerenchyma-fibres, which run free in the mesophyll, and branch out from the sclerenchyma of the veins, is a very general character, but more detailed statements on this subject are not given by the author. In the species which I have examined more thoroughly (*Chailletia Dichapetalum*, R. Br., *C. gelonoides*, Hook. f., and *Tapura guianensis*, Aubl.) these fibres are not present. In *C. Dichapetalum* the entire mesophyll contains large secretory cells which possess brown contents, and in the palisade-tissue mostly have the form of enlarged palisade-cells, but in the spongy parenchyma have a rounded outline; these secretory cells were incorrectly interpreted by Barth (loc. cit., p. 506 and Fig. 11) as air-cavities ('lacunes probablement aérifères'). Large crystal-idioblasts with clustered crystals are found in the uppermost layer of the palisade-tissue of *Chailletia vitiensis*, Seem. The **epidermis** of the leaf either consists of one or many layers. Hypoderm is described by Barth in *Chailletia Benthamii*, F. Didr., and numerous species of *Tapura* and *Stephanopodium*. Mucilaginous cells occur in the epidermis of the leaf in *Tapura ciliata*, Gardn., and (according to Barth, loc. cit., pp. 516 and 498) in the hypoderm of species of *Stephanopodium* and *Tapura*. It may be added that cells with a mucilaginous membrane also occur in the primary cortex of the branches and in the outer ground-tissue of the petiole; in the latter tissue in *Tapura capitulifera*, Baill., *Stephanopodium Blanchetianum*, Baill., and *S. peruvianum*, Poepp. et Endl., Barth has met with peculiar cells, which have their membranes gelatinized on one side, and become secondarily thickened like stone-cells. **Stomata** occur only on the lower side of the leaf and have one or two subsidiary cells on each side parallel to the pore, in the species which I have examined with regard to this feature (*Chailletia Dichapetalum*, *C. gelonoides*, *C. pedunculata*, DC., *Tapura amazonica*, Poepp. et Endl., *T. guianensis*). The vascular bundles of the smaller **veins** are accompanied by sclerenchyma in *Chailletia Dichapetalum* and *C. gelonoides* and also in *Tapura guianensis*. The **hairy covering** consists exclusively of simple unicellular clothing hairs. The latter (Fig. 46) are mostly sclerenchymatous and vary in length. In the cases investigated by me (*Chailletia mossambicensis*, Klotzsch, *C. pedunculata*, *C. vestita*, Benth., and *Tapura amazonica*) the walls of the clothing hairs are characterized by small conical or blunt papillae, which become solid during the thickening of the wall of the hair. They are either (*T. amazonica*) distinct, recalling a similar feature in certain Amarantaceae (*Iresine*), &c., or are only just visible, and in that case are noticeable merely as small jagged irregularities on the longitudinal wall.

The following facts require mention regarding the structure of the **axis**. The cork originates quite generally in the subepidermal layer of cells, according to Barth. A sclerotic phelloderm frequently occurs; frequently also stone-cells are present in the more or less collenchymatous primary cortex. Isolated

[1] Anat. comp. de la tige et de la feuille des Trigoniacées et des Chailletiacées, Bull. de l'Herbier Boissier, t. iv, 1896, pp. 497–520; Barth has examined very numerous species of the three genera (*Chailletia*, *Stephanopodium*, *Tapura*); his statements, however, leave something to be desired: Barth did not recognize the uniform type of stoma; the species, in which he found the various features, are not systematically quoted in connexion with the latter.

[2] See also Solereder, Holzstr., 1885, p. 96 and Engler, in Nat. Pflanzenfam., 3. Teil, Abt. 4, 1896, p. 346.

groups of bast-fibres appear in the pericycle throughout [1]. The secondary bast not uncommonly (*Stephanopodium Blanchetianum* and *S. peruvianum*) contains sclerenchyma. In *Chailletia crassifolia*, Chodat, the bast is said to penetrate the xylem-mass in places in the manner of bast-wedges. The xylem consists of vessels, which have lumina of no great size (maximum diameter = ·048 mm.), of wood-prosenchyma, wood-parenchyma and medullary-ray-tissue. According to Barth, side by side with narrower (uniseriate to quadriseriate) medullary rays, broad rays (as much as ten cells wide) occasionally also occur, the cells of which are irregularly arranged. The perforations of the vessels are usually simple and elliptical ; in addition to these in the secondary wood of *Tapura guianensis*, Aubl., scalariform perforations with fairly numerous thin bars are found. The wood-parenchyma is usually rather abundant. According to Barth the wood-prosenchyma has bordered pits on its walls in all the members of the Order. I have myself been able to observe distinct and typical, though not numerous, bordered pits in *Chailletia gelonoides* only. The thickness of the walls and the narrowness of the lumina of the wood-fibres, to say the least, render the observation of the borders difficult.

OLACINEAE.

1. Review of the Anatomical Features. The Olacineae as delimited by Bentham and Hooker in the 'Gen. Plant.' are such a heterogeneous Order in relation both to their exomorphic and endomorphic features, that I must here restrict myself to a bare enumeration of the anatomical features.

With regard to the leaf-structure it may first be noted that the stomata are either surrounded by several ordinary epidermal cells, or are accompanied by two or several subsidiary cells parallel to the pore (*Opilia*). Special structural features of the leaf occurring in this Order are: gelatinization of the upper epidermis (species of *Apodytes*, *Gomphandra* and *Mappia*) ; development of hypoderm on the upper side of the leaf (species of *Anacalosa* and *Cathedra*) ; papillose differentiation of the epidermis on the lower side (species of *Apodytes*, *Erythropalum*, *Liriosma*, and *Olax*) ; occurrence of solitary crystals (*Phlebocalymna Griffithiana*, Mast.) or of clustered crystals (species of *Erythropalum* and *Strombosia*) in the epidermis of the leaf ; occurrence of spicular cells (species of *Cathedra* and *Heisteria*) or of sclerenchyma-fibres (species of *Desmostachys*, *Discophora*, *Endusa*) free in the mesophyll.

As to the structure of the axis it may first be pointed out that the members of this Order, so far as is known, possess wood-prosenchyma with bordered pits. The perforations of the vessels vary. In the tribe Olaceae, exclusively simple (*Olax*, *Cathedra*) as well as exclusively scalariform (*Heisteria*, *Endusa*) perforations occur. The investigated representatives of the Opilieae and Phytocreneae have simple perforations only, those of the Icacineae always have scalariform perforations, either alone or side by side with simple openings. Diversity is also shown in the size of the vessels, in the pitting of the walls of the vessels where they are in contact with ray-parenchyma, and in the amount of the wood-parenchyma. The development of cork takes place superficially. In the pericycle one finds either a composite and continuous ring of sclerenchyma (in most of the genera, see structure of axis), or isolated bundles of bast-fibres (*Cardiopteris*, *Olax*), or a loose ring of bast-fibres (*Pyrenacantha*).

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[1] *Chailletia edulis*, Kurz forms the only exception according to Barth. But this species has already been transferred by Kurz to the Olacinean genus *Sarcostigma* as *S. edule* (see Hooker, Fl. Brit. Ind., i. p. 594), and consequently does not come into consideration.

The differentiation of the internal secretory organs is very varied. Thus the following forms occur: mucilage-cells (species of *Agonandra* and *Opilia*), secretory cells with resinous contents (*Opilia amentacea*, Roxb.), non-articulated laticiferous tubes (*Heisteria*), articulated laticiferous tubes (*Endusa* and *Cardiopteris*), schizogenous secretory cavities (*Endusa*, *Coula*), lysigenous mucilage-spaces (axis of *Phytocrene macrophylla*, Bl.), mucilage-canals (*Trematosperma* and (?) *Cardiopteris*).

Oxalate of lime is excreted in the leaf in the form of ordinary solitary or clustered crystals or crystal-sand (the last only in *Apodytes andamanica*, Kurz, and *Gomphandra*), or is absent (Opilieae). In the genera of the Opilieae (*Cansjera*, *Agonandra*, *Lepionurus* and *Opilia*), in place of oxalate of lime, cystoliths occur, the cells which bear the latter (lithocysts) lying in twos or several together (Fig. 47, *A–B*). On the other hand, in the genera of the Olaceae (*Ximenia*, *Olax*, *Liriosma*, *Cathedra*, and *Schoepfia*), solitary silicified cells or groups of them are common in the mesophyll.

The hairy covering usually consists of simple unicellular hairs of varied length. Special forms of hairs are the multicellular trichomes of species of *Cansjera* (Fig. 48, *A*), which are branched like a stag's horn, and the unicellular hairs of *Cardiopteris* and *Platea* (Fig. 48, *B–C*), described below. In *Phytocrene* tufted hairs occur, in *Platea* (Fig. 48, *D*) multicellular peltate hairs lastly, in *Gonocaryum pyriforme*, Scheff. (Fig. 48, *E–F*), Haberlandt has met with peculiar structures to be classed with the hairs, which serve as hydathodes and are single metamorphosed epidermal cells.

Anomalous structure of the axis has been observed in some Phytocreneae. *Phytocrene* and *Pyrenacantha* have wedges of bast in the xylem-mass, similar to those of certain Bignoniaceae. In *Phytocrene* a second anomaly is added in the thicker branches, viz. the occurrence of successive rings of growth (Fig. 49). Interxylary phloem is met with in *Sarcostigma* and *Chlamydocarya*; in *Iodes*, *Natsiatum*, and other Phytocreneae, unequal increase of the wood is found, which may become obliterated when the axis attains a greater thickness; besides this, in *Iodes tomentella*, Miq., there are medullary, inversely orientated, vascular bundles.

2. Structure of the Leaf. The very varied structural features of the leaf have formed the subject of a treatise by Edelhoff[1], from which the following statements are chiefly taken.

In most members of the Order the **leaf-tissue** is bifacial in structure. Edelhoff describes centric leaf-structure in *Ximenia coriacea*, Engl., *Olax stricta*, R. Br., and *Opilia amentacea*, Roxb., only. In most cases the stomata are found only on the lower side of the leaf; they occur on both sides in *Ximenia*, species of *Olax*, and in *Cansjera parvifolia*, Kurz. Edelhoff makes no statement as to the grouping of the epidermal cells which border on the guard-cells. It may therefore be mentioned that, according to my own observations, the stomata are surrounded by 3 or 4 epidermal cells (not differentiated by their shape) in *Lasianthera apicalis*, Thw., by 3 in *Gomphandra axillaris*, Wall., and *Alsodeiopsis Weissenborniana*, F. Br. et K. Schum., while the stomata of *Opilia amentacea*, Roxb., are accompanied by 2–4 subsidiary cells, which are parallel to the pore. Mucilaginous **epidermal cells** have been observed by Edelhoff in all the species of *Gomphandra* and *Apodytes* investigated by him as well as in *Mappia oblonga*, Miers. In the three investigated species of *Cathedra* and in *Anacolosa Griffithii*, Hook. Catal. the presence of

[1] The following genera were investigated: in tribe i, Olaceae: *Aptandra*, *Heisteria*, *Ximenia*, *Olax*, *Liriosma*, *Erythropalum*, *Strombosia*, *Cathedra*, *Anacolosa*, *Schoepfia*; in tribe ii, Opilieae: *Cansjera*, *Agonandra*, *Lepionurus*, *Opilia*; in tribe iii, Icacineae: *Gomphandra*, *Desmostachys*, *Apodytes*, *Mappia*, *Poraqueiba*, *Emmotum*, *Icacina*, *Phlebocalymna*, *Villaresia*, *Cassinopsis*; Edelhoff's researches did not extend to tribe iv, the Phytocreneae.

ypoderm on the upper side of the leaf is mentioned by Edelhoff. The epi-ermal cells on the lower side of the leaf are papillosely differentiated in ıany species of *Olax* (*O. acuminata*, Wall., *O. Benthamiana*, Miq., *O. nana*, Vall., *O. Phyllanthi*, R. Br., *O. scandens*, Roxb., *O. stricta*, R. Br., but not in *. Wightiana*, Wall., and *O. zeylanica*, L.), also, in *Liriosma Pohliana*, Engl., *rythropalum scandens*, Bl., and *Apodytes dimidiata*, E. Mey. In certain species ranched, or rarely (*Heisteria Spruceana*, Engl.) unbranched, spicular cells are ound in the mesophyll (e. g. in *Heisteria brasiliensis*, Engl., *H. citrifolia*, Engl., *I. cyanocarpa*, Poepp. et Endl., *H. densifrons*, Engl., *H. flexuosa*, Engl., *H. Kappleri*, Sagot, *H. laxiflora*, Engl., *H. ovata*, Benth., *H. Spruceana*, Engl., ut not in *H. acuta*, Engl.; and in *Cathedra acuminata*, Miers), or one neets with sclerenchyma-fibres, which have a free course, e. g. in *Desmo-tachys Renschii*, O. Hoffm., *Discophora guianensis*, Miers, and, according to Radlkofer, in *Endusa punctata*, Radlk., and according to Haberlandt in *Gono-caryum pyriforme*, Scheff. As regards the structure of the smaller **veins**, their vascular system is either enclosed by a ring of sclerenchyma, or is accompanied only by a few sclerenchyma-fibres or by collenchymatous tissue. The detailed structure of the sclerenchyma-fibres in the veins of *Emmotum* is remarkable; the walls of the fibres are provided with numerous oblique, slit-shaped and spirally arranged pits in such a manner that the fibres appear as though spirally thickened. Edelhoff has observed strongly developed terminal tracheides in species of the genera *Ximenia*, *Schoepfia*, *Agonandra*, and *Phlebo-calymna*. According to Van Tieghem in the genera of Opilieae (*Agonandra*, *Cansjera*, *Lepionurus*, and *Opilia*), a branched anastomosing system of bundles, composed of reticulately or spirally thickened and lignified cells ('tissu d'irri-gation'[1]) runs between the veins, similar to that which has been observed in the leaves of *Cycas* and *Podocarpus*.

Internal **secretory organs** are present in very varied forms, but only have a small range within the Order. They occur as: cells with mucilaginous membranes, secretory cells, non-articulated laticiferous tubes, articulated laticiferous tubes, schizogenous secretory cavities, lysigenous gum-receptacles and mucilage-canals.

Mucilage-cells have been observed by Edelhoff in the spongy parenchyma of *Agonandra brasiliensis*, Miers, and *Opilia umbellulata*, Baill., secretory cells with a finely granular secretion, which stains with iodine-solution and is with difficulty soluble in alcohol, in the lowest layer of the spongy parenchyma in *Opilia amentacea*, Roxb. Non-articulated laticiferous tubes are found, according to Radlkofer and Edelhoff, in all the investigated species of *Heisteria*. They have resin-like contents, and in some cases run independently of the veins freely in the spongy tissue, in other cases they accompany the bundle-system of the veins. They are frequently to be recognized even with a lens as a network of transparent lines in the leaf. Other laticiferous elements, which, although without distinct articulation, must be interpreted as articulated laticiferous tubes on account of their reticulate connexions, have been observed by Radlkofer in the genus *Endusa* (with the species *E. punctata*, Radlk.), which he has rescued from oblivion. In this plant the latici-ferous vessels traverse not only the leaves, but also the branches and the parts of the flower. In the branch they are present in the bast; in the leaves they chiefly accompany the larger vascular bundles, but are occasionally also found free from the latter in the leaf-tissue. Like those of *Endusa*, the laticiferous elements (investigated in detail by Thouvenin) of the genus *Cardiopteris* (with the species *C. lobata*), in which a 'succus aqueus' had previously been mentioned by Bentham and Hooker, must also be classed among the articulated laticiferous tubes[2]; for

[1] In part perhaps identical with Edelhoff's terminal tracheides?

[2] Engler (Sitz.-Ber. Berliner Akad., 1893, p. 267) describes the secretory organs of *Cardiopteris* in question as 'apparently non-articulated laticiferous tubes' ('wie es scheint, ungegliederte Milch-saftschläuche').

they are narrow tubular elements, which are only slightly branched and exhibit (this being the essential feature) transverse anastomoses. The laticiferous tubes of *Cardiopteris* form three separate systems in the stem—in the peripheral part of the pith, in the bast, and in the primary cortex, and occur also in the petiole and the veins of the leaf. According to Radlkofer the occurrence of apparently schizogenous secretory cavities, provided with a small-celled epithelium, in the genus *Endusa*, which is also characterized by the possession of laticiferous tubes, is very remarkable. These secretory cavities are found in the spongy parenchyma; after protracted action of eau de Javelle, a portion of their contents becomes coloured blue in consequence of the conversion of a body (indican?), contained in the secretion, into indigo, while another portion disappears. According to Van Tieghem, schizogenous secretory receptacles are present also in the genus *Coula*, Baill., which is referred to the Olacineae, in the tissue of the leaf and cortex. Lysigenous receptacles with mucilage and gum have been observed by Robinson in the soft tissues of the stem of *Phytocrene macrophylla*. They form large cavities, filled with a tenacious gum-like substance. The secretion possesses strong fluorescence; thus it appears pale brown by transmitted light, bluish-white by reflected light. Whether this secretion has anything to do with the sap which the living plant yields on injury, and to the abundance of which the genus *Phytocrene* owes its name, is very doubtful, as many stems—especially when young, but sometimes older specimens also—are destitute of the secretory receptacles in question. Lastly, the mucilage-canals of *Trematosperma*, observed by Engler, may be mentioned in connexion with

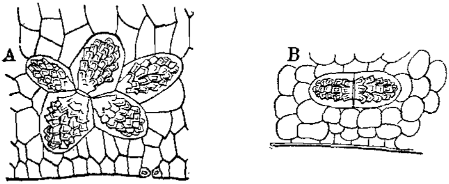

FIG. 47. A–B, A group of cystoliths and a pair of cystoliths from the mesophyll of *Cansjera timorensis*. —After Van Tieghem.

the gum-receptacles of *Phytocrene*; it does not appear clearly from Engler's statements whether the 'lysigenous canals,' which are described by him in *Cardiopteris*, and arise secondarily on the inner side of the vascular bundles of the axis, should also be classed here.

Oxalate of lime is present in the leaf in the form of solitary crystals, clustered crystals, or crystal-sand, or is absent (the latter in the genera of Opilieae: *Cansjera, Agonandra, Lepionurus* and *Opilia*, which are characterized by cystoliths; see below).

Edelhoff describes:—I. solitary crystals in: *Aptandra, Heisteria*, species of *Olax, Erythropalum*, species of *Cathedra, Anacolosa*, species of *Mappia*, species of *Poraqueiba, Icacina, Phlebocalymna*, species of *Villaresia*; II. clustered crystals in: *Ximenia*, species of *Olax, Liriosma, Erythropalum, Strombosia, Cathedra, Desmostachys, Apodytes acutifolia*, Hochst., species of *Mappia, Discophora*, species of *Poraqueiba, Emmotum*, species of *Villaresia*; III. crystal-sand in: *Gomphandra* (in this case sometimes surrounding solitary crystals) and *Apodytes andamanica*, Kurz.—In the epidermis of the leaf solitary crystals are present in *Phlebocalymna Griffithiana*, Mast., clustered crystals in *Erythropalum scandens*, Bl., and *Strombosia javanica*, Bl.

Two very noteworthy anatomical features in this Order are the occurrence of cystolith-like structures, encrusted with carbonate of lime, and of silicified cells. The **cystolith-like** excretions (Fig. 47, *A–B*) are present only in the members of the tribe Opilieae (*Cansjera, Agonandra, Lepionurus*, and

Opilia[1]). They were discovered almost simultaneously by Edelhoff and Valeton; recently they have also been described by Van Tieghem. In the leaf the cystolith-containing cells are arranged in pairs or in groups of several; at corresponding points of the common wall between two of these cells a stalk arises; this is either impregnated with silica or lignified, variously shaped at its end, and of varied breadth, and around it crystallization of carbonate of lime takes place, occasionally in the form of beautiful tabular crystals. According to Van Tieghem these cystoliths are also found in the parenchymatous tissues of the axis, and it is specially noteworthy that he even met with them in the wood (in *Cansjera*).

The silicified cells are described by Edelhoff in *Ximenia americana*, L., *X. coriacea*, Engl., in numerous species of *Olax*[2] (*O. acuminata*, Wall., *O. nana*, Wall., *O. scandens*, Roxb., *O. stricta*, R. Br., *O. Wightiana*, Wall., and *O. zeylanica*, L.), for *Liriosma* (*L. acuta*, Miers, *L. adhaerens*, Spruce, *L. grandiflora*, Engl., *L. ovata*, Miers, and *L. Pohliana*, Engl.), for *Cathedra Gardneriana*, Miers, *C. rubricaulis*, Miers, and in *Schoepfia* (*S. arborescens*, Roem. et Schult., *S. chrysophylloides*, Planch., *S. fragrans*, Wall., *S. jasminiodora*, Sieb. et Zucc.). They either form cell-rows, or cell-surfaces, or spherical cell-groups, or they may be present singly. Sometimes all their walls are silicified: the whole cell is silicified; or the thickening and silicification extend only to a portion of the cell-wall.

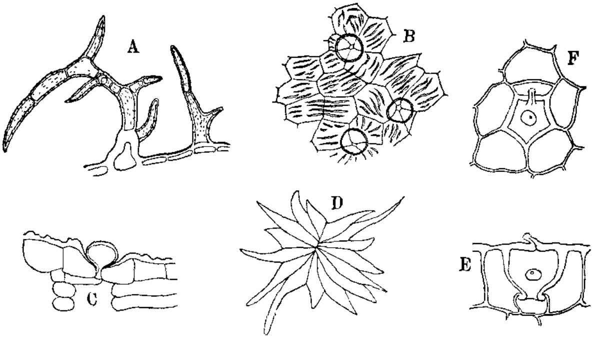

FIG. 48. Hairy covering of the Olacineae. A, *Cansjera parviflora*, Kurz; B–D, *Platea excelsa*, Bl.; E–F, Hydathodes of *Goniocaryum pyriforme*, Scheff.—A–D original, E–F after Haberlandt.

As regards the **hairy covering** of the leaf (Fig. 48) simple unicellular hairs of varied length, not uncommonly occur, according to Edelhoff's statements (species of *Liriosma*, *Mappia*, *Gomphandra*, *Apodytes*, *Poraqueiba*, *Discophora*, *Emmotum*, *Villaresia*). The trichomes of *Villaresia* are found in small

[1] The *Opilia Cumingiana*, Baill., cited by Edelhoff (loc. cit., p. 135), in which cystolith-like structures are absent in the leaf, is not an *Opilia*, but belongs to the genus *Champereia*. (Regarding this genus, which in part likewise possesses cystolith-like structures and which has been removed by recent authors to the Olacineae, see the appendix to the Santalaceae, to which it is referred by Bentham and Hooker.)

[2] Blenk (loc. cit.) wrongly interpreted the siliceous cells of the species of *Olax* as stone-cells.

depressions of the surface of the leaf. Edelhoff has described multicellular hairs, branched like a stag's horn (Fig. 48, *A*), as occurring in *Cansjera parvifolia*, Kurz, and *C. scandens*, Roxb. From personal observation I can add two further special forms of hairs, both of which occur in *Platea excelsa*, Bl.: firstly, short compressed-spherical unicellular hairs (Fig. 48, *B–C*), which have quite a small insertion in the epidermis and possess a fairly thick external wall, and secondly, peltate hairs with jagged outline (Fig. 48, *D*), and thin-walled ray-cells which meet along a median line. Likewise, according to my own observations, I may mention the tufted hairs of *Phytocrene bracteata*, Wall., and the unicellular hairs, which are swelled like bladders, pointed at their ends, and apparently have a glandular function, of *Cardiopteris Rumphii*, H. Baill., γ *lobata*, Baill. (Zollinger, No. 446, Java, Herb. DC.).

With the trichomes we may also class the curiously differentiated epidermal cells (Fig. 48, *E–F*), which were discovered by Haberlandt in *Goniocaryum pyriforme*, Scheff., and which physiologically represent hydathodes—organs for the excretion and absorption of water. Each of these epidermal cells is differentiated into three parts; firstly, into (*a*) a very short hair-like portion, which springs eccentrically from the thick external wall, is traversed by a delicate canal and is mucilaginous at its tip, while the epidermal cell itself (which is provided with a large nucleus and a fairly well developed primordial utricle) is divided into (*b*) an upper part, which has the form of a 4–6-sided funnel with its narrow opening downwards, a thick cellulose ring forming a border to the latter, and (*c*) a lower thin-walled bladder-like portion. The small ovoid bodies, which occur at the ends of the veins in the leaf of *Trematosperma cordatum*, Urb., and species of *Pyrenacantha* (*P. scandens*, Harv., and *P. malvaefolia*, Engl.), also serve for the excretion of water. According to Engler, these glandular bodies enclose a cavity, which is elongated like a canal and opens on the exterior by means of a narrow slit-shaped aperture at the tip of the gland; the epidermis bears short, club-shaped, very thin-walled trichomes in the lower part of the cavity. The wall of the cavity which forms the main mass of the gland consists chiefly of parenchyma, and around the canal this shows an arrangement in radial cell-rows, and is traversed in its outer portion by bundles of tracheides, which are inserted on the vascular bundles of the veins of the leaf (cf. Fig. 8, Engler, loc. cit.).

3. Structure of the Axis. The account I give of the structure of the **wood** is essentially based on the observations[1] set forth in my 'Holzstruktur.' The medullary rays vary in breadth. The vessels have lumina of various sizes. The width of the vessels is usually of medium dimensions (diameter = ·078 mm.); the vessels of the twining or climbing species of *Phytocrene* and *Natsiatum*, for example, have a much larger lumen (diameter as much as ·22 mm.). The pitting of the vessel-wall, where it is in contact with parenchyma of the medullary rays, is not always the same: bordered pits alone occur on this part of the wall in the species of *Olax*, *Cansjera*, *Opilia*, *Gomphandra*, *Desmostachys*, *Apodytes* and *Sarcostigma* that I have examined, while in *Heisteria* and *Endusa* there are chiefly simple pits, and in *Poraqueiba* simple as well as bordered pits. Lastly, on the vessel-walls touching the ray-parenchyma in *Cathedra rubricaulis*, Miers, side by side with bordered pits, large circular simple pits are met with in places; these latter appear like simple circular vessel-perforations and in some cases are even apparently of the nature of true perforations. The perforations of the vessels present just as little uniformity as the anatomical characters of the wood already mentioned. Among the members of the tribe Olaceae, investigated by me, *Olax* and *Cathedra* possess only circular or elliptical simple perforations; *Heisteria* and according to Radlkofer *Endusa* also, have exclusively scalariform perforations. In the

[1] Species of the following genera were investigated: *Heisteria*, *Olax* and *Cathedra* of the tribe Olaceae; *Cansjera* and *Opilia* of the tribe Opilieae; *Gomphandra*, *Desmostachys*, *Apodytes* and *Poraqueiba* of the tribe Icacineae; *Phytocrene* and *Sarcostigma* of the group Phytocreneae.

investigated species of the tribes Opilieae and Phytocreneae I have met with simple perforations only. Engler also describes the latter type exclusively in his groups Iodeae (*Natsiatum*, *Iodes*, *Polyporandra*) and Phytocreneae (*Trematosperma*, *Miquelia*, *Pyrenacantha*, *Phytocrene*, *Chlamydocarya*), as well as in *Cardiopteris*, genera which are referred by Bentham and Hooker to the Phytocreneae. Scalariform perforation of the vessels is characteristic of the Icacineae. The representatives of this tribe which I have investigated have either scalariform perforations throughout (*Apodytes*, *Poraqueiba*), or the scalariform and simple types side by side (*Gomphandra*, *Desmostachys*). Scalariform perforations always occur, although they are sometimes restricted to the neighbourhood of the primary wood, e. g. in *Desmostachys Renschii*, Hoffm. A much larger number of genera of Icacineae (namely *Cassinopsis*, *Villaresia*, *Chariessa*, *Platea*, *Alsodeiopsis*, *Leptaulus*, *Lasianthera*, *Stemonurus*, *Urandra*, *Apodytes*, *Raphiostyles*, *Desmostachys*, *Pennantia*, *Kummeria*, *Mappia*, *Leretia*, *Icacina*, *Emmotum*, and *Poraqueiba*) has been examined in this respect by Engler, and here also scalariform perforations were always found. Spiral striation of the walls of the vessels has been observed in *Opilia amentacea*, Roxb. The wood-parenchyma is developed in very varied amount, very abundantly for example in *Cathedra rubricaulis*; in *Opilia amentacea*, on the other hand, not specially so. The wood-prosenchyma, so far as it has been examined (by Engler as well as by me), bears bordered pits ; the borders of the pits, however, are not always easy to see, e. g. in *Cathedra rubricaulis*, where the wood-fibres have thick walls and narrow lumina. Lastly, it remains to be mentioned that the innermost part of the wood in all the Phytocreneae is poor in vessels and forms what is called ring-wood (see Robinson and Engler, loc. cit.).

The following facts are known as to the structure of the **cortex**. The formation of cork takes place in the epidermis in the cases investigated (species of *Opilia*, *Lasianthera*, *Apodytes*, *Pennantia*, *Phytocrene*, *Iodes*, *Trematosperma*). The cork-cells sometimes (*Lasianthera*, *Apodytes*, *Pennantia*) have strongly thickened inner tangential walls. The pericycle varies in its constitution. It either contains isolated bundles of bast-fibres (*Olax scandens*, Roxb., *Cardiopteris lobata*, Wall.), or a loose ring of bast-fibres (*Pyrenacantha volubilis*, Hook.), or very frequently a composite and continuous ring of sclerenchyma (in *Opilia amentacea*, Roxb., *Gomphandra axillaris*, Wall. ; according to Engler, in *Villaresia paniculata*, Miers, *Platea excelsa*, Bl., *Leptaulus daphnoides*, Benth., *Gonocaryum gracile*, Miq., *Emmotum fagifolium*, Desv. *Poraqueiba guianensis*, Aubl., *Urandra apicalis*, Thw., *Raphiostyles Poggei* Engl., *Pennantia Endlicheri*, Reiss., also in *Iodes* and *Polyporandra*, and according to Van Tieghem, quite generally in *Cansjera*, *Opilia*, *Agonandra* and *Lepionurus*). According to Van Tieghem, secondary bast-fibres are completely absent in the Opilieae. In the young twining branches of the Phytocreneae the middle part of the primary cortex is frequently differentiated as collenchyma. In the older stems of *Phytocrene macrophylla*, Bl., and *Chlamydcarya Soyauxii*, Engl., this collenchyma graduates outwards into sclerenchymatous sheath (Engler).

Anomalous structure of the axis is only known with certainty in representatives of the tribe Phytocreneae. According to H. Schenck, the thick liane stems of *Olax scandens*, Roxb., and *Cansjera Rheedii*, Gmel., appear to be normal in structure. In the few climbing Icacineae, likewise, no definite anomalies of stem-structure are known. Possibly, however, the two stems, collected by H. Schenck and mentioned by him in his discussion of the Icacineae, may belong to this tribe ; they possess narrow secondary rings of wood and bast similar to those found in the genus *Securidaca* among the Polygaleae.

Of the anomalies demonstrated in the Phytocreneae, the uneven development of the secondary wood must be placed in the first rank ; this is clear

apparent in the younger branches, but may become lost in older stems by the adjustment of cambial activity.

Robinson made a detailed investigation of this unequal development of the wood in *Iodes tomentella*, Miq., *I. ovalis*, Bl., and *Natsiatum herpeticum*, Buch.-Ham., and Engler has since shown that the same type occurs also in *Polyporandra* and in the Phytocreneae, Engl. (see above). In the Iodeae (*Iodes*, *Polyporandra*, and *Natsiatum*) the cambium produces abundant secondary wood with vessels, having wide lumina, on the exterior of the above-mentioned 'ring-wood' (which encloses the primary vessels and the pith internal to the latter), but only on the two opposite sides, which lie in the long axis of the elliptical transverse section ('interfoliar sides,' in so far as they bear no leaves at the node next above); between these, on the broad sides ('foliar sides') of the branch, the formation of wood lags; here only a little unlignified (*Iodes tomentella*, Miq.) or lignified (*I. ovalis*, Bl., *Polyporandra Hansemanni*, Engl.) xylem-tissue is formed. According to Engler, it is quite general in the Phytocreneae, Engl., for the development of wood with large vessels to take place exclusively or principally on the interfoliar sides, while on the foliar sides the bast-tissue is more abundantly developed.

In *Iodes tomentella* (but not in *I. ovalis*) a second anomaly appears, seated in the pith, in the form of medullary vascular bundles, which are inversely orientated with regard to the position of their xylem and phloem, and which by their structure, as well as by their origin, recall the well-known medullary bundles of *Tecoma radicans*. Even in the young stem of *I. tomentella* the pith is encroached upon by two strips of soft bast, which lie opposite to one another, are directed towards the narrow sides of the stem, and grow in thickness by means of a special cambium; these cambial layers only produce some few tracheides towards the outer side, but on the inner side give rise to abundant phloem which, opposite each cambium, is formed in two portions separated by a strip of parenchyma.

Sarcostigma Kleinii, Wight et Arn., as I have already pointed out in my 'Holzstruktur,' possesses another anomaly in the structure of its stem, namely interxylary phloem, and the same occurs in *Chlamydocarya Soyauxii*, Engl., and *C. Thomsoniana*, Baill., according to Engler's recent observations. According to Chodat, the islands of soft bast in *Sarcostigma* are given off from the inner side of the cambium.

In the genus *Phytocrene* (Fig. 49) the occurrence of wedges of bast, which penetrate into the xylem-mass, is specially characteristic.

These bast-wedges have been described by earlier authors (Mettenius, Mohl, De Bary) in an undetermined species, and have recently been very accurately investigated by Robinson in *Phytocrene macrophylla*, Bl. Their formation proceeds in the following manner. At first, during growth in thickness, the stem produces ring-wood with small-lumened vessels. Then the formation of grooves begins; longitudinal strips of the cambium diminishing their wood-producing activity, whilst in the grooves of the wood thus resulting so much the more soft bast is formed externally. In this manner the cambium is split up into two kinds of longitudinal strips, of which those found at the bottom of the grooves produce but little wood, poor in vessels, while forming much bast-tissue; the other strips of cambium, lying between the increasing wedges of bast, produce much wood, rich in large vessels on the inner side, and on the outer side only a small amount of soft bast. The plates of bast (Fig. 49, *B*) consist of sieve-tubes with wide lumina and oblique, scalariform sieve-plates[1], companion cells, fibrous cells[2] with thick walls, and short-membered sclerenchyma. The soft bast, formed on the outer side of the projections of the wood, contains only sieve-tubes and bast-parenchyma. The number of the wedges of bast amounts to 5–17 in *Phytocrene macrophylla*. From a systematic point of view it is worthy of note that I also met with the wedges of bast in question in the two species represented in the Munich herbarium, *P. bracteata*,

[1] According to Engler sieve-plates of this kind are very common throughout the Phytocreneae.

[2] Engler interprets these fibrous cells as 'tracheides' for reasons which are not known to me, and describes the plates of bast in *Phytocrene* as 'leptom-hadrom-strands.' Engler has observed similar 'tracheides' in the bast-tissue of the remaining Phytocreneae, Engl., hence these elements or the leptom-hadrom-strands respectively are characteristic of the Phytocreneae, Engl.

Wall., and *P. hirsuta*, Bl., and likewise in the following species seen in the De Candolle herbarium: *P. gigantea*, Wall. (Wallich no. 4946), *P. luzoniensis*, Baill. (Llanos), *P. palmata*, Wall., and *P. oblonga*, Wall. (Wallich no. 4948).

The older stems of *Phytocrene macrophylla* are further complicated, according to De Bary and Robinson, by the appearance of successive new peripheral rings, consisting of plates of wood and bast (Fig. 49, *A*). The first secondary annular zone, according to De Bary, arises in the bast; according to recent and more exact statements made by Robinson it is partly derived from the parenchyma of the pericycle, partly from the outer portion of the phloem. The origin of the cambium of the succeeding rings could not be determined with certainty.

In conclusion, the anomalously constructed stems of *Trematosperma* and *Pyrenacantha* are related to *Phytocrene* in structure. The tuberous stem of

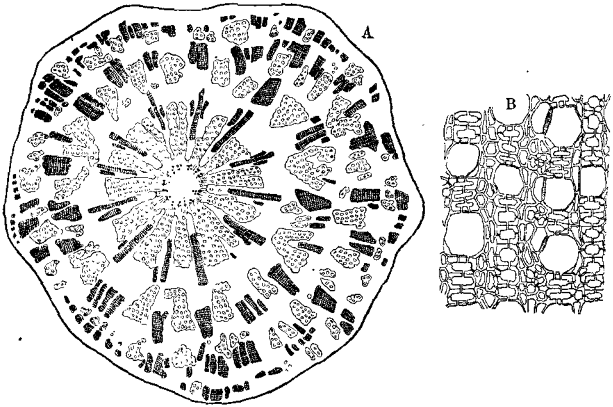

FIG. 49. *Phytocrene macrophylla*, Bl. A, Transverse section through the axis (magnification about 2 : 1). B, Transverse section through a piece of a bast-wedge.—After Robinson.

Trematosperma cordatum, Urb., which grows to a thickness of three metres, according to Engler shows formation of secondary wood- and bast-bundles in the same manner as in *Phytocrene macrophylla*; the cambium, however, arises much more irregularly than in the latter plant. In *Pyrenacantha scandens*, Harv., Robinson has demonstrated the occurrence of (5) wedges of bast, which penetrate the xylem-mass and have the same structure as those of *Phytocrene*. According to my own casual observation in the De Candolle herbarium, *Pyrenacantha volubilis*, Hook. (Thwaites no. 1024) also has bast-wedges of like nature three in number.

NOTE.—The genus *Scytopetalum*, Pierre, which is united by Engler with th Olacinean genus *Rhaptopetalum*, Oliv., to form the Order Scytopetalaceae, accordin to Engler, possesses the following anatomical features. The xylem contains narro medullary rays, vessels with very steep scalariform perforations, tracheides, an libriform. The bast is stratified into hard and soft bast. Small vascular bundle

run in the primary cortex. The leaf-structure is bifacial. The mesophyll is irregularly traversed by fibre-like spicular cells.

Literature: Mohl, Bot. Zeit., 1855, p. 875.—De Bary, Vergl. Anat., 1877, especially pp. 592 and 606.—Blenk, Flora 1884, p. 348, separate copy, p. 68.—Solereder, Holzstr., 1885, pp. 96-8.—Radlkofer, Sitz.-Ber. Münch. Akad., 1886, pp. 307-14.—Edelhoff, Vergl. Anat. d. Bl. der O., Engler, Bot. Jahrb., Bd. viii, 1887, pp. 100-53.—Valeton, Crit. Overz. der O., Groningen, 1886.—Engler, in Natürl. Pflanzenfam., iii. Teil, Abt. 1, 1889, p. 231.—Robinson, Stammanat. v. *Phytocrene macrophylla*, Bot. Zeit., 1889, pp. 645, 661, 677 and 693 et seq. and Taf. ix.—Robinson, Stem-struct. of *Iodes tomentella*, etc., Ann. Jard. bot. de Buitenzorg, vol. viii, 1890, pp. 95-121 and pl. xviii, xix.—Thouvenin, Lacticif. dans une O., le *Cardiopteris lobata*, Bull. Soc. bot. de France, 1891, pp. 129, 130.—Chodat, Atti Congresso bot. internaz. Genoa, 1892.—Engler, in Natürl. Pflanzenfam., iii. Teil, Abt. 5, 1893, pp. 234-9.—Engler, Verw. anat. Merkm. bei d. syst. Glied. d. Icacin., Sitz.-Ber. Berliner Akad., 1893, pp. 247-69 and Taf. ii.—H. Schenck, Anat. d. Lianen, 1893, pp. 78-80.—Van Tieghem, *Cansjera*, *Champereia* et la fam. des Opiliac., Ann. sc. nat., sér. 7, t. xvii, 1893, pp. 249-57 and pl. 9.—Haberlandt, Sitz.-Ber. Wiener Akad., Bd. ciii, Abt. 1, 1894, p. 498 (10) et seq. and Tab. i; and Sitz.-Ber. deutsch bot. Gesellsch., 1894, p. 367 et seq. and Tab. xxiv.—Van Tieghem, Bull. Mus. d'hist. nat., 1895, Paris, p. 167.—Engler, in Natürl. Pflanzenfam., Nachtr. u. Reg., Teil ii-iv, 1897, pp. 142, 145 and 242.

ILICINEAE.

1. Review of the Anatomical Features. The Ilicineae are excellently characterized by the scalariform perforations of their vessels, the prosenchyma with bordered pits, the bordered pitting of the walls of the vessels, where the latter are in contact with parenchyma, the lack of a special type of stomatal apparatus, and by the absence of internal as well as external glands. To what extent a composite and continuous ring of sclerenchyma in the pericycle and superficial development of cork are characteristic of the Order remains to be proved. Oxalate of lime is found in the form of ordinary solitary and clustered crystals. The pubescent hairy covering, which only rarely occurs, is formed by small unicellular trichomes.

The leaves, so far as they have been investigated, are of bifacial structure throughout, and bear stomata on the lower surface only. A special character of certain species of *Ilex* is the occurrence of small cork-warts (Fig. 50) on the lower surface of the leaf, which, owing to their presence, appears beset with small black dots; further, the occurrence of a many-layered epidermis, of hypoderm and of mucilaginous epidermal cells in the leaf.

2. Structure of the Leaf[1]. The leaves of the Ilicineae are bifacial in structure. The upper **epidermis** either consists of a single (e.g. in *Ilex theezans*, Mart., var. *gracilior*, Warm.) or of 2 or 3 layers, in consequence of the appearance of division-walls parallel to the surface of the leaf (e.g. in *Ilex theezans*, Mart., var. *typica*, Loes., and *I. affinis*, Gardn., vars. *genuina*, Loes. and *rivularis*, Loes.). The large-celled hypoderm, which is developed beneath the upper epidermis of *Ilex Aquifolium*, is not derived from the epidermis, but from the ground-tissue of the leaf according to Pfitzer[2], and my own investigation. In some of the species of *Ilex* mucilaginous epidermal cells occur; e.g. in *Ilex theezans*, Mart., var. *gracilior*, Warm., in which the gelatinization extends to nearly all the cells of the upper and also to individual cells of the lower epidermis, the mucilaginous cells of the upper epidermis penetrating deeply into the tissue of the leaf; isolated cells in the lowest layer of the many-layered epidermis of *Ilex theezans*, var. *typica*, and *I. affinis*, vars. *genuina* and

[1] Literature: Loesener, Vorstud. zu einer Monogr. der Aquifoliaceen, Diss., Berlin, 1890, pp. 33-7; Areschoug, Blad. Anat., Minnesskrift, Lund, 1878, p. 26 et seq. and Tab. v, vi; De Bary, Vergl. Anat., 1877; Lalanne, Feuilles persist., Act. Soc. Linn. de Bordeaux, sér. 5, t. iv, 1890, p. 54 and pl. ii; Kronfeld, Natürl. Pflanzenfam., iii. Teil, Abt. 5, 1892, p. 181; Loesener, Beitr. zur Kenntnis der Matepfl., Ber. deutsch. pharmaceut. Gesellsch., 1896, separate copy, 34 pp.

[2] Mehrschichtige Epidermis und Hypoderma, Pringsheim's Jahrb., Bd. viii, 1872, p. 51.

rivularis[1], also possess mucilaginous inner walls. Another noteworthy structural feature, which characterizes the lower epidermis of the leaf in the two varieties of *Ilex affinis* mentioned, is the considerable thickening and pitting of the inner walls of its cells. In *Ilex dipyrena* the epidermis contains chlorophyll. The cuticle, which clothes the epidermis and is partly the cause of the glossy appearance of the leaf, varies in thickness; while in *Nemopanthes* and the subgenus *Prinus* it is very thin, it attains a very considerable thickness in the subgenus *Aquifolium*. Apart from the cuticle, which is sometimes provided with undulated striations, two cuticular layers are characteristic of certain species, e. g. *Ilex Aquifolium*, *I. insignis*, *I. latifolia* and *I. crenata* (in the last-named species, at any rate, at the margin of the leaf). **Stomata** are found only on the lower side of the leaf; special subsidiary cells are wanting. In species provided with coriaceous leaves the palisade-tissue consists of two or more layers, while in *I. decidua* (subgenus *Prinus*) it is one-layered. The spongy parenchyma also shows varied differentiation. In *I. decidua*, for example, it forms a uniform tissue without large lacunae. The opposite extreme is found in the leaves of *I. insignis* and *I. latifolia*, in which the cells of the spongy tissue are separated by large intercellular spaces. In the **veins** sclerenchyma is either scantily or rather abundantly developed. Thus, the sheath of bast is completely missing in the smaller veins of *I. decidua*, while in the species, which are furnished with coriaceous leaves, a sheath of hard bast is met with on the lower side of the vascular bundles of the veins (*I. insignis*, *I. latifolia*, *I. Aquifolium*, *I. Dahoon*), or on both sides (*I. paraguariensis*).

A **hairy covering** is rare in this Order. Glandular hairs are completely absent. Where a hairy covering occurs, as for example on the young branches and petioles of *I. Aquifolium* or, according to Loesener, on the leaf of *I. Pseudothea*, Reiss., it consists of short unicellular hairs, the lumina of which are almost or quite obliterated.

In the leaf, **oxalate of lime** appears to occur only in the form of clustered crystals, and solely in the mesophyll[2]. Occasionally (*Ilex theezans*, Mart., var. *typica*, Loes.) the crystal-cells of the leaf-tissue contain, besides a clustered crystal, numerous fairly large crystalline granules of the same salt.

The black dots (Fig. 50) on the lower side of the leaf of certain species of *Ilex* are also worthy of note. They are structures resembling lenticels (cork-warts) and consist of a hemispherical group of cells, the component cells having suberized membranes, and radiating out from the centre of the hemisphere in radial rows[3]. E. Bachmann has observed these cork-warts in *Ilex Aquifolium*; Loesener states that they serve as a diagnostic character for some species (e.g. *I. amara*, Loes., *I. conocarpa*, Reiss., and *I. diuretica*, Mart.), while in other species (e.g. *I. theezans*, Mart., *I. Cuyabensis*, Reiss., and *I. Paraguariensis*, St. Hil.) they are either absent or are only developed exceptionally.

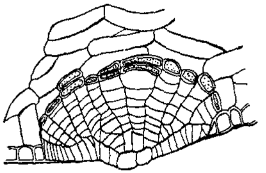

Fig. 50. Cork-wart from the lower side of the leaf of a Paraguay tea-plant.—Original.

[1] Loesener in his treatise on 'Mate' has wrongly interpreted the mucilaginous inner membrane of the epidermis as cells ('weitlumige Wasserspeicherzellen'; see Loesener's correction in Abh. bot. Ver. d. Mark Brandenburg, 1897, p. 68). This correction is especially noteworthy to any one attempting to determine from what plant a given kind of 'mate' is derived by means of Loesener's work.

[2] The statement in the works of De Bary, Kronfeld, &c., as to the occurrence of oxalate-crystals in the epidermal cells of the leaf of *Ilex paraguariensis* is incorrect.

[3] See E. Bachmann, Korkwuch. auf Bl., Pringsheim's Jahrb., Bd. xii, 1879–81, p. 209 et seq.

In concluding the description of the lamina, the mechanical strengthening of the margin of the leaf may be referred to; it is either caused by a mere thickening of the cuticle, or besides this there is a tissue consisting of cells, which contain chlorophyll but at the same time are sclerenchymatously thickened (*I. insignis*), or there is a stereom-sheath (formed by true sclerenchyma-fibres) of varied strength and form (*I. Aquifolium, I. dipyrena, I. cornuta*); reference may also be made to the spinous leaf-teeth[1] of certain species, e.g. *I. Aquifolium*, with converging strands of sclerenchyma.

According to Plitt[2], the **petiole** of *Ilex* contains an arc-shaped fibro-vascular system of one or several isolated bundles.

3. STRUCTURE OF THE AXIS[3]. The **wood** is firstly characterized by the scalariform perforations of the vessels, which have very numerous bars; contrary to Möller's statement they occur even in *Ilex Aquifolium*, and Loesener has demonstrated them not only in numerous species of *Ilex*, but also in *Nemopanthes canadensis*, DC. The vessels have a lumen of varied size; in *Ilex Aquifolium* their maximum diameter amounts to only ·045 mm.; *Ilex anomala*, on the other hand, is, according to Loesener, distinguished by vessels with very wide lumina. It should be noted with reference to the structure of the walls of the vessels that, accompanying the bordered pits, spiral thickening of the wall also occurs quite generally, and further, that the vessel-wall bears bordered pits, where it is in contact with the parenchyma of the medullary rays. According to Loesener, the walls of the large vessels of *I. anomala* possess scalariform, instead of the ordinary, bordered pits. The medullary rays are 1–4, rarely more, cells in breadth (in *Ilex Aquifolium* sometimes as much as 10 cells broad, according to Möller); according to Loesener, medullary rays, which are a single cell in breadth, only appear to occur in *I. verticillata*. The wood-parenchyma is fairly well developed. The wood-prosenchyma has bordered pits and is frequently also spirally thickened.

The structure of the **cortex** has been examined only in *Ilex Aquifolium*. In this species the cork takes its origin in the epidermis, and is composed of unusually thick-walled cork-cells. The primary cortex is collenchymatous and at first contains clustered crystals, which subsequently disappear and are replaced by solitary crystals; later on stone-cells also appear in the primary cortex. Isolated groups of bast-fibres are present in the pericycle of the young branches, and finally become united by stone-cells into a composite and continuous ring of sclerenchyma. According to Möller both bast-fibres and crystal-sacs are absent from the secondary bast, while the parenchyma of the bast is filled with drops of oil.

CYRILLEAE.

The following account may be given of the anatomy of this Order from my own investigation[4] of the leaf and axis in *Cyrilla racemiflora*, L. and *Cliftonia nitida*, Gaertn. f.

The mesophyll in both species consists of palisade-tissue only. The epidermal cells have straight lateral walls. Mucilaginous epidermal cells have been

[1] See Mittmann, Verh. d. bot. Ver. der Prov. Brandenburg, xxx, 1888, pp. 61 and 62.

[2] Plitt, Blattstiel, Diss., Marburg, 1886, p. 50.

[3] Literature: Chalon, Tig. lign. dicotyléd., i. Mém., 1867, pp. 49, 50; Gris, Moelle, Nouv. Arch. du Mus. d'hist. nat., t. vi, 1870, pp. 257, 258; Möller, Holzanat., Denkschr. Wiener Akad., 1876, pp. 91 and 387 respectively; Möller, Rindenanat., 1882, pp. 288–90; Solereder, Holzstr., 1885, pp. 98, 99; Loesener, loc. cit., pp. 31–3. [Loesener, Ilex p., in Notizbl. k. bot. Gart. u. Mus. z. Berlin, 1897, n. 10.]

[4] See also Solereder, Holzstruktur, 1885, p. 99, and Gilg, in Natürl. Pflanzenfam., iii. Teil, Abt. 5, 1892, pp. 179, 180.

observed in both species. The stomata are found only on the lower side of the leaf, and are surrounded each by a rather large number of ordinary epidermal cells. The dull appearance of the lower surface of the **leaf** of *Cliftonia nitida* is caused by high, irregularly arranged cuticular ridges. The vascular bundles of the veins are accompanied by sclerenchyma, which in *Cyrilla racemiflora* is developed in the form of a ring, in *Cliftonia nitida* chiefly in connexion with the xylem. Oxalate of lime occurs in the form of clustered and ordinary solitary crystals. A hairy covering is wanting, and so are internal secretory organs.

Regarding the structure of the **wood**, as in the allied Ilicineae, special stress should be laid on the scalariform perforations of the vessels, which often have numerous bars (20–30), as well as on the wood-prosenchyma with typical bordered pits. The vessels are numerous, being fairly uniformly scattered through the whole of the wood, and having lumina of inconsiderable size (diameter = ·03–·054 mm.). The bordered pits, which are present on the parts of the vessel-walls in contact with the parenchyma of the medullary rays, are not always distinct. The medullary rays are narrow, but, nevertheless, become as much as 4 cells broad externally. The wood-parenchyma is not developed in abundance.

In both species the development of cork takes place in the innermost part of the primary **cortex** (in the parenchymatous pericycle ?), and is apparently accompanied by formation of phelloderm. In *Cyrilla racemiflora* the cork contains cells which are sclerosed on one side (on the inner tangential wall). Owing to the internal formation of cork the primary cortex, which, especially in *Cliftonia nitida*, contains numerous sclerosed parenchymatous cells with wide lumina, is soon thrown off. Bast-fibres are absent both from the pericycle and the bast. In place of them sclerosis of the parenchyma in the outer part of the bast takes place after the commencement of the development of cork.

CELASTRINEAE.

This Order has so far been little investigated anatomically. The following features should be pointed out as applying to the species investigated : superficial origin of the cork, bordered pitting of the prosenchymatous groundwork of the wood, the tendency to the formation of scalariform perforations in the vessels, the lack of a uniform type of stoma, and the absence of external glands. Oxalate of lime occurs in the form of solitary and clustered crystals. In the genus *Wimmeria* the occurrence of a caoutchouc-like substance in cells of the bast has been observed ; in *Kokoona* resin-cells (?) occur in the leaf.

Investigations on the structure of the **leaf** were undertaken by Stenzel [1], the results of which were shortly abstracted by Loesener (loc. cit.), while the original work has not appeared up to the present time. For my own general survey I have investigated *Elaeodendron glaucum*, Pers., *Celastrus articulatus*, Thunb., and *Euonymus theaefolius*, Wall. In these three species the stomata possess no special subsidiary cells. Solitary crystals are stated by Loesener to occur in the epidermal cells of the leaf of *Cassine* [2] section *Euelaeodendron*, Loes. ; in *Elaeodendron glaucum* I found small epidermal cells, which were isolated or aggregated in groups, each being filled by one clustered crystal, or more rarely by a single solitary crystal. According to Loesener

[1] See Prantl's Arb. aus dem bot. Garten zu Breslau, Heft 1.

[2] Loesener, following Kuntze's example, transfers the species of *Elaeodendron* to the generic name *Cassine*.

gelatinization of the epidermis of the leaf has been observed in *Perrottetia*, and is also present in *Goupia glabra*, Aubl.; a hypoderm of 1 or 2 layers occurs in *Rhacoma* and some species of *Cassine*, and also in *Euonymus theaefolius*. In *Maytenus* and *Lophopetalum* the mesophyll contains only solitary crystals, in *Euonymus*, *Putterlickia*, *Schrebera* and *Cassine* (section *Eucassine*, Loes.), clustered crystals occur, while in other genera no constancy in this respect is found. The black dots, present on the lower side of the leaf of *Kokoona zeylanica*, Thw., are supposed by Gilg to be caused by large resin-glands (= probably resin-cells) differentiated in the epidermis and in the mesophyll. A hairy covering seldom occurs in this Order. Glandular hairs have not been observed[1]. On the veins of the leaf of *Celastrus articulatus* I found simple unicellular hairs in the form of long finger-shaped papillae; in *Fraunhofera multiflora*, Mart., one meets with rather long, simple hairs, which are unicellular, or, owing to thin division-walls, uniseriate.

The **petiole** has been examined by Plitt in the genera *Catha*, *Celastrus*, *Elaeodendron*, and *Euonymus*. A transverse section shows an arc-shaped fibro-vascular system of one or of several vascular bundles of unequal size.

With regard to the structure of the **wood**, which I have investigated in species of *Fraunhofera*, *Elaeodendron*, *Celastrus*, *Maytenus*, *Euonymus*, and *Microtropis*, the following account, which takes the remaining literature into consideration, may be given. The medullary rays of the wood are of varied breadth (as much as six cells in breadth in *Celastrus monospermus*, Roxb., and, according to H. Schenck, also in other species of *Celastrus*, e. g. *C. paniculatus*, Willd., and *C. stylosus*, Wall., only 2-seriate in *Euonymus europaeus*, L.); the xylem-vessels vary in the size of their lumina (maximum diameter between ·027 mm.—*Fraunhofera multiflora*, Mart.—and ·075 mm.). The perforations of the vessels are usually simple. More rarely scalariform perforations occur, either exclusively or side by side with simple perforations. According to Loesener, the species of *Cassine* belonging to the section *Euelaeodendron*, Loes., are characterized by scalariform perforations; *Cassine glauca*, (Pers.) O. Kuntze alone possesses simple perforations side by side with scalariform ones; the species of the two sections *Eucassine*, Loes., and *Mystroxylon*, Eckl. et Zeyh., on the other hand, only have simple perforations. Scalariform perforation of the vessels has also been observed: by me in the primary wood of *Celastrus monospermus*, Roxb., and recently in *Goupia glabra*, Aubl. (exclusively scalariform), and by Stenzel in *Kurrimia*. The vessel-wall is provided with bordered pits, even where it is in contact with the parenchyma of the medullary rays. Spiral thickening of the vessel-wall occurs in *Euonymus europaeus*, L. The wood-prosenchyma, which forms the groundwork of the wood, has, as a rule, distinctly bordered pits; side by side with this latter type, wood-prosenchyma with simple pits is often also found (*Elaeodendron*, *Euonymus*, *Fraunhofera*, *Maytenus*, *Microtropis*); it consists of cells with fairly wide lumina, and is sometimes septate owing to scattered division-walls. The wood-parenchyma is usually little developed and restricted to the neighbourhood of the vessels; in *Microtropis bivalvis*, Wall., it occurs in greater abundance, and in the form of uniseriate tangential bands.

Our knowledge of the structure of the **cortex** is almost restricted to the two genera *Celastrus* and *Euonymus*, which have been investigated especially by Möller. In these the origin of the cork is superficial; it is formed in the epidermis in all the species of *Euonymus* examined by Möller, Douliot, and J. E. Weiss, but subepidermally in the species of *Celastrus*. The cork-cells

[1] On the other hand the leaf-teeth are sometimes secretory. Reinke (in Pringsheim's Jahrb., Bd. x, 1876, p. 142) states that colleters occur on the leaf-teeth of *Catha cassinoides*, and that they consist of a few axile rows of cells and of an external layer; the cells of the latter are wedge-shaped in the upper part of the colleter and are the seat of the secretion.

of *Euonymus* have thin walls; those of *Celastrus* are sometimes sclerosed on one side. Primary groups of bast-fibres are wanting in *Euonymus obovatus*, Nutt., and *E. verrucosus*, Scop.; *E. latifolius*, Mill., and *Celastrus scandens*, L., on the other hand, have primary groups of bast-fibres, the component elements of which in *Celastrus* are characterized by the peculiar cracks which they show in transverse section. According to my own casual observation, the primary groups of bast-fibres in *Goupia glabra*, Aubl. are united by stone-cells into a composite and continuous ring of sclerenchyma; according to Radlkofer, the same occurs in the genus *Llavea*, Liebm., which has been renamed *Neopringlea* by Watson, but its position in the Natural System is not yet quite certainly established. According to Möller, no bast-fibres are found in the secondary bast in *Celastrus scandens*, L., but in *Euonymus obovatus*, Nutt. sclerenchymatous fibrous cells, groups of thin-walled compressed fibrous cells and peculiarly metamorphosed fibres[1] occur in this tissue; I did not meet with the last-named elements in herbarium-branches of the species in question, and they need further investigation. The soft bast also contains chambered fibres with clustered crystals and sieve-tubes with scalariform sieve-plates. In the soft bast of the branches, as well as in that of the leaf-bundles of all the species of *Wimmeria*, Radlkofer describes the occurrence of cells, which are filled with an elastic caoutchouc-like substance, and recall the similar elements in certain species of the genus *Salacia*, belonging to the Hippocrateaceae (q. v.). It may also be noted that the peculiar cork-warts of the cortex of *Euonymus verrucosus* are not lenticels, according to Stahl, as they are not developed below stomata, but are rather corky outgrowths of the cortical parenchyma, which elevate the epidermis.

The **pith** is homogeneous in the species of *Euonymus* investigated by Gris. The lianes among the Celastrineae, e.g. the North American *Celastrus scandens*, L. and the East Indian *Celastrus*-lianes, cited by Gamble, are, almost throughout, normal in structure. Only in an undetermined *Celastrus* from the Neilgherries an external grooving of the stem occurs, according to Jussieu, and similarly in *Euonymus tingens*, according to Lindley.

Literature: Jussieu, Arch. Mus. d'hist. nat., t. iii. 1843, p. 117.—Lindley, Veg. Kingd., vol. i, 1848, p. 213, fig. 40.—Chalon, Tiges lign. dicotyléd., i. Mém., Gand, 1867, pp. 13, 14.—Gris, Moelle, Nouv. Arch. Mus. d'hist. nat., t. vi, 1870, p. 258 and pl. xv.—Stahl, Lenticellen, Bot. Zeit., 1873, p. 616.—Möller, Holzanat., Denkschr. Wiener Akad., 1876, pp. 90 and 386.—Penzig, Crist. del Rosanoff nelle C., Nuov. Giorn. bot., vol. xii, 1880, pp. 24-31 and tab. i.—Möller, Rindenanat., 1882, pp. 284-7.—Solereder, Holzstr., 1885, pp. 99-101.—Plitt, Blattstiel, Diss., Marburg, 1886, p. 50.—Douliot, Ann. sc. nat., sér. 7, t. x, 1889, p. 359.—Lalanne, Feuilles persist., Act. Soc. Linn. Bordeaux, sér. 5, t. iv, 1890, p. 84 and pl. v.—J. E. Weiss, Korkb., Denkschr. Regensburg. bot. Gesellsch., 1890, p. 65.—Loesener, in Natürl. Pflanzenfam., iii. Teil, Abt. 5, 1892, pp. 192, 193.—H. Schenck, Anat. d. Lianen, 1893, p. 131.—Radlkofer, Bot. Gazette, 1893, p. 199 and Natürl. Pflanzenfam., iii. Teil, Abt. 5, 1895, p. 366.—Wittlin, Kalkoxalattasch., Bot. Centralbl. 1896, iii, p. 68.

HIPPOCRATEACEA.

Of the Hippocrateaceae the two genera *Hippocratea* and *Salacia* have been investigated in a general and preliminary manner. A systematic investigation of the Order is desirable, and from what is already known it promises very good results.

The following may be pointed out as characters common to the two genera mentioned above: lack of a special type of stoma and of external glands, superficial origin of cork, absence of a ring of sclerenchyma in the pericycle,

[1] 'Compact, flexible, vermiform fibres ·105 mm. in thickness and of very varied length (not uncommonly exceeding 1 mm.), having their surface densely covered with small angular pits'; loc. cit., Fig. 103.

predominantly simple perforations in the vessels, bordered pitting of the prosenchymatous groundwork of the wood and excretion of oxalate of lime in the form of ordinary solitary and clustered crystals. As generic characters the occurrence of a hypoderm in the leaf and of crystal-cells in the epidermis of the leaf, described by Stenzel in *Hippocratea*, but not in *Salacia*, in which hypoderm and crystal-cells are stated to be absent, require further examination. The distribution of caoutchouc-containing elements and tannin-sacs within the genus *Salacia* has likewise still to be determined. In *Salacia* anomalous stem-structure (Fig. 51) occurs; it consists in the appearance of successive rings of growth or of interxylary phloem (as in the *Strychnos*-type).

Our knowledge of the structure of the **leaf** in this Order at the present time rests on a few preliminary statements of Stenzel's[1], which are quoted by Loesener in the revision of the Hippocrateaceae for the 'Natürliche Pflanzenfamilien,' and on my own investigation of *Hippocratea arborea*, Roxb., *Salacia crassifolia*, Peyr., and *S. attenuata*, Peyr. Stenzel, or rather Loesener, describes in *Hippocratea* a 1- or 2-layered hypoderm, clustered and solitary crystals in the mesophyll and petiole, and solitary crystals in the epidermal cells of the leaf; in *Salacia* absence of hypoderm, occurrence of clustered crystals and absence of solitary crystals in the mesophyll and petiole, and absence of crystal-cells in the epidermis. As regards the species investigated by me, it was only in *Hippocratea arborea* that I met with a one-layered hypoderm on the upper side of the leaf, and in both upper and lower epidermis small cells, each filled by a clustered crystal (not a solitary crystal); these cells lie in groups, either two or several together, rarely singly. In the three species investigated by me the stomata are surrounded by several neighbouring cells. In the thick leathery leaf of *Salacia crassifolia* each portion of the palisade-tissue (which is uniformly developed below the epidermis on both surfaces) contains a system of sclerenchyma-fibres, which, running at right angles to the surface of the leaf, traverse the palisade-tissue, are connected with the vascular bundles of the veins by branches given off towards the interior, and also branch abundantly below the epidermis of both surfaces of the leaf. In the thinner, bifacially constructed mesophyll of *Salacia attenuata* solitary cells of the palisade and spongy parenchyma are sclerosed. With this tendency to the formation of spicular cells, the latter should occur more frequently in the thick leaves of this Order. I have not observed trichomes[2] in the species which I examined, but on the other hand I have found numerous cork-warts on the lower side of the leaf of *Salacia attenuata*.

Statements as to the ordinary structure of the axis are to be found in the works of Möller, Loesener, and Solereder; and regarding the anomalous structure of the stem especially in H. Schenck's work. With regard to the structure of the **wood**, the groundwork consists of prosenchyma with bordered pits, but is accompanied by simple-pitted prosenchyma in subordinate amount. The vessels have simple perforations; in *Salacia grandiflora*, Peyr., scalariform perforations with few bars are also found in the neighbourhood of the primary wood. The parts of the walls of the vessels which are in contact with ray-parenchyma are provided with bordered pits. In the herbarium-branches of both genera, which I have examined, the medullary rays are narrow. According to H. Schenck, thicker pieces of the stem of *Hippocratea ovata*, Lam., and of other species show broad medullary rays. The latter become broader externally in

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[1] See note 1 on p. 212.

[2] The abundant excretion of water on the leaves of *Salacia* (*S. melitocarpa*, Bl., and *S. oblongifolia*, Bl.) is caused neither by trichomes nor by water-pores, but is probably due to the fact that the epidermal cells possess what are called marginal pits, through which the water passes out (Haberlandt).

the same way as in *Aristolochia*; they divide the xylem-ring up into plates, and are further specially characterized by containing groups of stone-cells.

The structure of the **cortex** has been investigated by Möller in *Hippocratea indica*, Willd., by me in *H. arborea*, Roxb., *Salacia micrantha*, Peyr., and *S. grandiflora*, Peyr. The cork arises subepidermally in *Salacia micrantha* and *Hippocratea arborea*. In the thicker branches and stems of certain species of *Salacia*, e.g. *S. micrantha*, the cork-cells contain a reddish-yellow pigment, which is soluble in alcohol, according to Loesener. In the two species of *Salacia* cited the primary cortex is rich in branched and sometimes large stone-cells. A ring of sclerenchyma is not present in the pericycle. In *Hippocratea arborea* large isolated groups of compressed bast-fibres with white walls and wide lumina are found at the outer limit of the bast. Similar groups of cells, but consisting of tissue like horn-bast, are met with in the pericycle in the two species of *Salacia* cited. The soft bast of *Salacia micrantha* is specially noteworthy, as containing elements resembling laticiferous tubes, which have narrow lumina and clear, caoutchouc-like contents, soluble in chloroform. These caoutchouc-containing elements are present in such abundance that on breaking a branch the fragments of the branch remain connected by the tough elastic threads of caoutchouc. The same elements are also found in the veins of the leaf and can be recognized there also, even with the naked eye, by the threads which appear on breaking a piece of the leaf. The secretory elements in question are also present in the two pieces of stem, no. 347 and no. 519 of H. Schenck, which belong to species of *Salacia*, and which will be further discussed when describing the anomalous structure of the stem; they are, however, absent in *Salacia grandifolia*, in which the bast contains groups of tannin-sacs with fairly wide lumina, which are elongated in the vertical direction and in dry material are filled with brown contents. The morphological value of the caoutchouc-elements still remains to be determined, i.e. whether they are to be classed with the non-articulated laticiferous tubes, or whether, like the caoutchouc-cells of the genus *Eucommia*, which is referred to the Trochodendreae, they only arise secondarily and are not already formed as rudiments in the embryo. These details can only be determined developmentally in suitable material. It further remains to be shown, from a systematic point of view, how widely these caoutchouc-tubes are distributed within the genus *Salacia*, and whether they possess, as is to be supposed, systematic significance in the grouping of the species. The above are questions which may be suggested here. It remains to be mentioned that Möller describes the occurrence of regular stratification of the secondary bast owing to tangential plates of hard bast in the species, *Hippocratea indica*, which he investigated. Stenzel's statement that solitary crystals are characteristic of the cortex of *Hippocratea*, clustered crystals of that of *Salacia*, cannot be accepted, because *Hippocratea arborea* contains clustered crystals in its primary cortex and solitary crystals in its bast.

Among the cases of **anomalous stem-structure** we may mention in the first place the occurrence of a grooved xylem-mass in an undetermined Hippocrateaceous piece of stem, viz. H. Schenck's no. 305 (figured in loc. cit., Fig. 78 on Tab. VIII); the grooves in the xylem are filled up by soft bast-tissue. In the genus *Salacia* one either finds, as Fritz Müller was the first to observe, repeated formation of cambium in the pericycle and resulting secondary rings of growth, or interxylary phloem of the type occurring in *Strychnos*; these two anomalies are in certain species connected by intermediate types (Fig. 51, *A*–*C*).

In *Salacia*, in the first type now to be described, the secondary rings of growth only appear late, and are very broad, e.g. especially in the piece of stem (no. 347) which is represented by H. Schenck in Fig. 81 on Tab. VII, and

belongs to *S. brachypoda*, Peyr., or to an allied species. In the second case the successive cambial layers follow rapidly on one another, e.g. in the piece of stem (of an undetermined species) collected by H. Schenck under the number 519 and represented in his Fig. 83 on Tab. VII, and in *Salacia serrata*, Camb. (Fig. 51, *B*). Even in these two pieces of stem the phloem-portions do not form continuous rings, but are embedded in the wood in the form of bands and strands. This signifies, that complete successive replacement of the original cambium by new layers does not take place, but only a partial renewal of the cambium, according to the *Strychnos*-type, though still involving long tangential tracts. Thus a transi-

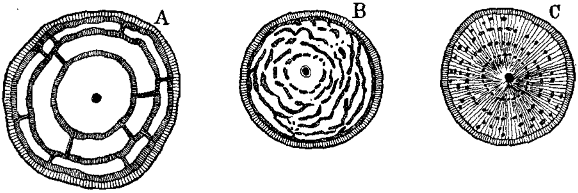

FIG. 51. Transverse sections of the anomalous axis of: A, *Salacia*? sp., Wood collection no. 590 of H. Schenck magnification 1½ : 1; B, *Salacia serrata*, Camb., magnification 1½ : 1; C, *Salacia*? sp., Wood collection no. 571 of H. Schenck, magnification slightly more than 1½ : 1.—All after H. Schenck.

tion is afforded to the case of the piece of stem, represented in Fig. 51, *C* (Schenck's no. 571) and to that of the herbarium-branches of *S. Regeliana*, K. Schum., of the Berlin and Munich collections, which show small interxylary islands of phloem, owing to the fact that in them, as in *Strychnos*, the successive partial renewal of the cambium is always restricted to small tracts of the cambium-ring. Lastly, reference may be made to the anomalous piece of stem collected by Dr. Ernst in Caracas, and described by Krüger as *Hippocratea scandens*, but the correct determination of which is very justly doubted by H. Schenck. The cortex of this specimen contains 15–18 small peripheral xylem-masses, anastomosing with one another, each of which grows in thickness by means of a cambium-ring of its own.

Literature: Fritz Müller, Bot. Zeit., 1866, p. 59 and Tab. iii.—Möller, Holzanat., Denkschr Wiener Akad., 1876, pp. 91 and 387.—Möller, Rindenanat., 1882, p. 288.—Krüger, Anom. Holzbild. Diss., Leipzig, 1884, pp. 34, 35.—Solereder, Holzstr., 1885, pp. 99–101.—Loesener, in Natürl Pflanzenfam., iii. Teil, Abt. 5, 1892, pp. 223, 224.—Radlkofer, Bot. Gazette, 1893, pp. 199, 200.—H. Schenck, Anat. d. Lianen, 1893, pp. 131–6 and Tab. vii.—Haberlandt, Sitz.-Ber. Wiener Akad. Bd. ciii, Abt. 1, 1894, p. 497 (9).

STACKHOUSIEAE.

A detailed investigation of the axis and leaf in this Order is still wanting. The following statements are based on a casual investigation of *Stackhousia spathulata*, Sieb., and *S. Brunonis*, Benth.

With regard to the structure of the wood the members of this Order are characterized by simple perforations in the vessels and by wood-prosenchyma which in part bears bordered, in part simple pits. At the outer limit of the bast in *S. spathulata* an interrupted ring of fibrous cells with yellow walls is present.

The leaves of *S. spathulata* have stomata on both sides; the guard-cells of the stomata are not accompanied by any special subsidiary cells.

A hairy covering is rare in this Order. The trichomes of *S. pubescens*, A. Rich. are ordinary unicellular hairs. Glandular hairs are absent. Oxalate of lime has not been observed. According to Pax[1], in the secondary cortex of the

[1] Pax, in Natürl. Pflanzenfam., iii. Teil, Abt. 5, 1893, p. 231.

rhizome, secretory cells with wide lumina occur; they are filled with dark brown contents, and are often enlarged in the tangential direction. They are of isodiametric or somewhat elongated tubular form, either solitary or a few together forming longitudinal series.

RHAMNEAE.

This Order has so far been little investigated anatomically [1]. According to the statements extant the following characters may be mentioned for the diagnosis of the Order: the usually simple perforation of the vessels, bordered pits on the vessel-wall, even where it is in contact with parenchyma of the medullary rays, simple pitting of the wood-prosenchyma, superficial development of the cork, the absence of a characteristic type of stoma and the frequent occurrence of mucilage-receptacles (mucilage-cells or mucilage-cavities of lysigenous origin) in the parenchyma of the cortex and of the veins of the leaf. Oxalate of lime is usually excreted in the form of ordinary solitary or clustered crystals, which, when situated in the mesophyll, occasionally give rise to transparent dots in the leaf. Small transparent dots in the leaf are also caused by the peculiar long needle-shaped crystals (styloids), which are extremely characteristic of the leaves of the genera *Crumenaria*, *Gouania*, and *Reissekia*, which belong to the Gouanieae. The following special features occurring in the leaf may be mentioned in addition to the above: the gelatinization of the epidermis in many members of the Order, the spicular cells, observed in *Scutia Commersonii*, Brongn., and the secretory cavities of *Karwinskia*, which cause transparent dots and are filled with resinous contents. Glandular hairs are wanting on the leaf-surface, but in many cases the leaf-teeth are differentiated as glands. The hairy covering consists chiefly of simple, unicellular or (owing to cross-walls) uniseriate trichomes; the Australian genera *Pomaderris*, *Trymalium*, *Spyridium*, and *Cryptandra*, are characterized by the possession of stellate hairs. Anomalies in the stem-structure have not been demonstrated, at least not with certainty.

The transparent dots in the **leaves**, and the anatomical characters connected with them have been thoroughly investigated by Blenk. With the purpose of determining the general features of the leaf-structure I undertook the investigation of the following representatives of the five tribes of the Order: *Ventilago calyculata*, Tul., *Zizyphus calophylla*, Wall., *Rhamnus saxatilis*, Jacq., *Ceanothus velutinus*, Dougl., *Colletia crenata*, Clos, *Gouania domingensis*, L., and *Reissekia cordifolia*, Endl. In all these species the stomata occur only on the lower side of the leaf. Each is, as a rule, surrounded by several epidermal cells in an irregular manner; in *Zizyphus calophylla* and *Rhamnus saxatilis* alone, stomata sometimes occur which are bordered on one or both longitudinal sides by one or more subsidiary cells parallel to the pore. Gelatinization of the epidermis of the leaf is very common. Blenk has met with it in species of *Ventilago*, *Paliurus*, *Microrhamnus*, *Berchemia*, *Rhamnus*, *Hovenia*, *Sageretia*, *Gouania*, and *Reissekia*; in addition to *Reissekia cordifolia*, I have also found it in *Colletia crenata*, and Volkens in *Zizyphus Spina Christi*, Willd. In the last-named plant, as in *Ceanothus velutinus*, the smaller veins are vertically transcurrent. Blenk has found spicular cells in the leaf-tissue

[1] The manuscript of the work on the anatomy of the Rhamneae announced by Prantl in Heft 1 of the Arbeiten aus dem Breslauer botanischen Garten is, according to Weberbauer (in the Natürl. Pflanzenfam.), completed, but still unpublished. A number of statements derived from it were published by Weberbauer (loc. cit.), and are therefore taken into account in what follows.

of *Scutia Commersonii*, Brongn. (*S. capensis*, Eckl. et Zeyh.), which cause transparent dots.

As regards the features presented by the **crystals** in the axis and leaf, it may in the first place be stated that oxalate of lime is usually found in the form of ordinary clustered and solitary crystals. Both kinds of crystalline elements may occur side by side; thus in *Ventilago maderaspatana*, for example, the veins are so to speak sheathed with solitary crystals, while clustered crystals are present in the mesophyll. In certain cases large clustered and solitary crystals, situated in the palisade-tissue, produce transparent dots in the leaf; viz., according to Blenk, solitary crystals in species of *Karwinskia*, *Rhamnus*, *Rhamnidium*, *Ceanothus*, and *Scutia*, and clustered crystals in species of *Rhamnus*, *Scutia*, and *Hovenia*. According to Blenk the genera *Crumenaria*, *Gouania*, and *Reissekia*, belonging to the Gouanieae (but not the fourth genus *Helinus*) are characterized by a special crystalline form of oxalate of lime, namely, by the possession of styloids. These styloids frequently lie parallel or obliquely to the surface of the leaf, but in some cases at right angles to it, and in that case they cause very small but distinct pellucid dots. It is interesting that in *Gouania domingensis*, which, like the rest of the species of *Gouania*, contains styloids in its leaf-tissue, the latter are not present in the axis but are replaced by clustered crystals (in the bast and in the primary cortex), as well as by ordinary short solitary crystals (in the neighbourhood of the secondary hard bast).

Of internal **secretory organs** the following have been observed: firstly, idioblasts, filled with brown contents, in the palisade-tissue of *Colletia crenata*; secondly, secretory cavities with brown contents, which are insoluble in alcohol, in the leaves of *Karwinskia glandulosa*, Zucc., in which they cause opaque dots; thirdly, mucilage-receptacles.

The mucilage-receptacles have recently been investigated by Walliczek and very thoroughly by Thouvenin and by Guignard and Colin, who extended the older statements of Th. Hartig (Forstl. Kulturpfl.), A. Vogl (Kommentar zur österr. Pharmakopöe), Flückiger (Pharmakognosie), Höhnel and Solereder. According to Guignard and Colin, the mucilage-receptacles occur in species of *Rhamnus*, *Hovenia*, *Ceanothus*, *Paliurus*, *Zizyphus*, and *Gouania*; on the other hand, they were not met with in the investigated species of *Berchemia*, *Sarcomphalus*, *Alphitonia*, *Colubrina*, *Phylica*, *Noltia*, *Pomaderris*, *Colletia*, *Cryptandra*, and *Trevoa*. In general the mucilage-receptacles are not characteristic of the genus; thus they occur only in a certain number of the species of *Rhamnus*, and, in some of these again, only in the axis and leaf, in the others only in the leaf. The positions in which the mucilage-receptacles occur are the inner portion of the primary cortex and the pith in the axis, and the parenchyma of the larger leaf-veins and of the petiole. The mucilage-receptacles are either cells with a mucilaginous membrane (sometimes of the same size as the cells surrounding them, but usually larger), or they are cavities, which arise in a lysigenous manner (often from groups of the mucilaginous cells). According to Guignard, the mucilage-cavities must not be confounded with the lacunae, which are sometimes formed by the splitting apart of bands of cells in the cortex. They often have a layer resembling an epithelium around them, so that, without taking their developmental history into consideration, they might very easily be regarded as schizogenous secretory receptacles. The growth in thickness of the branches has some effect on the mucilage-cavities of the cortex, so that the latter become compressed and flattened in the tangential direction. In the pith, on the contrary, the mucilage-receptacles retain their form, and sometimes become enlarged to such an extent through the extension of the gelatinization that they become visible to the naked eye (*Rhamnus Frangula* and *Paliurus aculeatus*). In my 'Holzstruktur' I have already described large medullary mucilage-receptacles of this kind, which are of the nature of canals, as occurring also in *Ventilago maderaspatana*, Gaertn., *Paliurus australis*, Gaertn. (=*P. aculeatus*, Lam.), and *Zizyphus calophylla*, Wall.

With regard to the **hairy covering**, it has already been stated above

that external glands are not present on the surface of the leaf, but that the leaf-teeth frequently show glandular differentiation. In accordance with this circumstance the resinous covering of the leaves of many species, e. g. *Ceanothus velutinus*, is probably to be attributed to an excretion from the glands of the leaf-teeth, this excretion being found not below but on the cuticle of the leaf-surface. The glandular leaf-teeth of *Rhamnus alpina* and *Noltea africana* have been investigated in detail by Reinke; in both plants the leaf-teeth bear a sharply marked apiculus, which in *Rhamnus alpinus* is composed of an axile strand of elongated cells and of small polygonal fairly isodiametric elements, in *Noltea africana* of an internal group of cells with wedge-shaped epidermal cells. Otherwise the hairy covering usually consists of simple trichomes, which vary in length, have thick or thin walls, and are unicellular, or, owing to the development of thin or thick division-walls, are multicellular. The four nearly-allied genera, which are characterized by the possession of stellate hairs, have already been mentioned above.

The **petiole** has been investigated by Plitt in species of *Rhamnus* only. Its transverse section shows an arc-shaped fibro-vasculat system of one or more vascular bundles.

The structure of the **wood** was investigated by me in species of *Ventilago, Paliurus. Zizyphus, Colletia, Discaria, Gouania, Reissekia,* and *Rhamnus*. The medullary rays of the wood are of varied breadth; the vessels vary in the size of their lumina (maximum diameter = ·03–·15 mm.). Spiral thickening is present on the walls of the pitted vessels in *Colletia spinosa*, Lam., *Rhamnus Frangula*, L., and *R. cathartica*, L., and, according to Krause, also in *Zizyphus vulgaris* and *Adolia* (= *Scutia*) *buxifolia*. The walls of the pitted vessels, where they are in contact with parenchyma of the medullary rays, are generally provided with bordered pits; the bordered pits in the corresponding positions in *Gouania glandulosa*, Boiv., are less distinct, their inner apertures being wider. The perforations of the vessels are almost always simple; in *Zizyphus calophylla*, Wall., and, according to Krause, in *Phylica*, scalariform perforations with few bars have been observed besides the simple perforations. The wood-parenchyma is little developed. The wood-prosenchyma has simple pitting.

The structure of the **cortex** has been little investigated[1] apart from the occurrence of the above-mentioned cortical mucilage-receptacles. The cork, as far as is known (*Rhamnus, Zizyphus*), arises subepidermally. In the pericycle isolated groups of bast-fibres are very frequently found (according to Guignard and Colin); in *Zizyphus orthocantha*, DC., however (according to Möller), there is a composite and continuous ring of sclerenchyma. The secondary bast contains bands of bast-fibres, which are developed in varying degree, and are usually sheathed by slightly sclerosed chambered fibres with solitary crystals. In addition to the solitary crystals, clustered crystals sometimes (*Rhamnus*) occur in the secondary bast. The medullary rays of the cortex in *Rhamnus* are filled with yellow contents (rhamnoxanthin, frangulin), which are coloured red by alkalies. Finally, it may be mentioned that the species of *Colletia* with reduced leaves, e. g. *C. ferox*, Gill. et Hook. and others, are characterized by abundant development of assimilatory parenchyma and by the occurrence of numerous stomata in the epidermis of the branch.

The nature of the **pith** has been investigated by Gris only in some species of *Rhamnus*; in these the pith is heterogeneous.

Anomalies of stem-structure are not yet known with certainty in this Order. *Gouania urticaefolia*, Reiss., *Reissekia cordifolia*, Steud., and *Zizyphus Oenoplia*, Mill.—all three being lianes—are normal in structure. The only anomalous

[1] Möller's investigations extend only to species of *Gouania, Paliurus, Rhamnus* and *Zizyphus*.

stems are: a piece of stem described by Krüger and doubtfully referred to *Gouania*; and likewise a piece of an axis, belonging to the Marburg collection, which H. Schenck mentions; it is described as *Gouania domingensis*, but is wrongly determined. Both specimens possess secondarily formed strands of wood in the phloem.

Literature:—Chalon, Tig. lign. dicotyléd., i. Mém., Gand, 1867, pp. 14-16.—Gris, Moelle, Nouv. Arch. Mus. d'hist. nat., t. vi, 1870, pp. 268, 269.—Reinke, Sekretionsorg., Pringsheim Jahrb., Bd. x, 1876, pp. 140, 141.—Möller, Holzanat., Denkschr. Wiener Akad., 1876, pp. 92, 93 and 388, —Höhnel, Sekretionsorg., Sitz.-Ber. Wiener Akad., Bd. lxxxiv, Abt. 1, 1881, pp. 591, 592.—Möller, Rindenanat., 1882, pp. 290-4.—Blenk, Flora, 1884, p. 355 et seq., separate copy, pp. 68-73.—Krüger, Anomal. Holzbild., Diss., Leipzig, 1884, pp. 32, 33.—Schube, Blattarme Pfl., Breslau, 1885, pp. 9, 10.—Solereder, Holzstr., 1885, p. 101.—Plitt, Blattst., Diss., Marburg, 1886, p. 50.—Volkens, Aegypt.-arab. W., 1887, p. 115.—Thouvenin, Struct. des Rh., Bull. Soc. d. sc. de Nancy, sér. 2, t. ix, fasc. 22, 1888, Paris, 1889, pp. xxi, xxii, abstract in Just, 1889, i, p. 697.—Guignard et Colin, Rés. à gomme chez les Rh., Bull. Soc. bot. de France, 1888, pp. 325-7.—Douliot, Ann. sc. nat., sér. 7, t. x, 1889, p. 360.—Ross, Nuov. Giorn. bot., t. xxi, 1889, p. 232.—Lalanne, Feuilles persist., Act. Soc. Linn. Bordeaux, sér. 5, t. iv, 1890, p. 106.—J. E. Weiss, Korkb., Denkschr. Regensb. bot. Gesellsch., 1890, p. 65.—H. Schenck, Anat. d. Lianen, 1893, pp. 141, 142.—Walliczek, Pringsheim Jahrb., Bd. xxv, 1893, p. 260 et seq.—Weberbauer, in Natürl. Pflanzenfam., 3. Teil, Abt. 5, 1895, pp. 394, 395.—Wittlin, Bot. Centralbl., 1896, iii, p. 100.—Kuhla, Phelloderm, Bot. Centralbl., 1897, iii, p. 199.—[Sayre, *Frangula* and *Cascara* bark, Americ. Journ. of pharm., 1897, n. 3.]

AMPELIDACEAE.

1. Review of the Anatomical Features. The Ampelidaceae are characterized by the possession of raphides, the prevalence of simple perforations in the vessels, and wood-prosenchyma which bears simple pits and is frequently septate. The development of cork takes place either in a superficial layer of the cortex or in the pericycle. The pericycle is occupied by isolated bundles of hard bast or by a composite and continuous ring of sclerenchyma. The stomata do not possess any special subsidiary cells. Oxalate of lime, besides occurring as raphides, is excreted in the form of small acicular crystals and ordinary solitary or clustered crystals. Of internal secretory elements only mucilage-cells are found. The hairy covering is formed by simple unicellular or uniseriate trichomes, unicellular two-armed hairs and unicellular spherical glandular hairs with short stalks; to the last-named category also belong the pearl-glands to be described more fully below, and the glandular structures resembling small peltate scales (Fig. 52), which are similar to the pearl-glands. *Tetrastigma scariosum*, Pl., and other species of this genus possess a peculiar anomalous stem-structure (described by H. Schenck as 'repeated formation of cambium in the phloem').

2. Structure of the Leaf. Detailed investigations on the subject of the general leaf-structure are still wanting. In the two species investigated by me (*Vitis vinifera*, L., and *Leea acuminata*, Wall.) the **leaf-structure** is bifacial and the palisade-tissue consists of one layer. In both these species the stomata are surrounded by three or more ordinary epidermal cells. In *Vitis vinifera* the stomata are restricted to the lower side of the leaf; in *Leea acuminata* they also occur in the neighbourhood of the veins in the upper epidermis, which is differentiated in a slightly papillose manner. In both the species named above, the vascular bundles of the larger veins contain no sclerenchyma.

The features presented by the **crystals** in the leaf are more accurately known. The characteristic form of the crystals is that of raphides; the sacs containing them can very frequently be recognized with a lens or even by the naked eye as transparent dots or fine striae. Blenk met with raphide-sacs in all the Ampelidaceae investigated by him, belonging, if we take into considera-

tion the more recent systematic literature[1], to the genera *Vitis*, *Ampelocissus*, *Pterisanthes*, *Tetrastigma*, *Parthenocissus*, *Ampelopsis*, *Rhoicissus*, *Cissus*, and *Leea*; similarly d'Arbaumont also found them in the axis of the numerous species which he examined. The raphide-sacs vary in length. Besides the raphide-needles, they contain a varying amount of mucilage[2]. Side by side with the raphides, clustered crystals also frequently occur in the mesophyll. The latter crystals sometimes, especially in species of *Leea*, attain a considerable size, and thus likewise give rise to transparent dots, e.g. in *Leea acuminata*, Wall. It may be added that a third type of transparent dots in the leaf of the Ampelidaceae is, according to Blenk, caused by large mucilage-cells. Blenk met with these in *Vitis ficifolia*, Bunge, *Parthenocissus quinquefolia*, Planch. ('*Ampelopsis hederacea*, Michx.'), *Tetrastigma serrulatum*, Planch. ('*Cissus capreolata*, Don'), and numerous American as well as certain African and Asiatic species of *Cissus*; according to Walliczek, they also occur in the cortex of *Parthenocissus quinquefolia*. As mucilage-containing raphide-cells occur in this Order, the idea is suggested that the mucilage-cells in question may possibly be 'raphide-sacs without raphides,' and it would follow that their mucilage would belong to the contents, as in raphide-cells, instead of being derived from the membrane, as in the Malvaceae; developmental proof of this has, however, still to be obtained.

The **hairy covering** has been examined especially in the stem by d'Arbaumont. It consists chiefly of clothing hairs. Of widespread occurrence are simple uniseriate trichomes, which either have blunt or pointed ends, and the cells of which are more or less distinctly articulated in certain cases. Side by side with the simple uniseriate hairs, simple unicellular hairs sometimes occur in the same species (*Cissus striatus*, Ruiz et Pav.). The dense hairy covering of the lower side of the leaf of *Ampelocissus tomentosa*, Planch., resembling a spider's web, is formed by very long unicellular ribbon-shaped hairs; d'Arbaumont observed these trichomes also on the branch of *Cissus adnata*, Wall., *Pterisanthes cissoides*, *Vitis coriacea*, Shuttlew., *V. lanata*, Roxb., *V. rupestris*, Scheele and others. The occurrence of unicellular two-armed hairs is deserving of notice; their exact distribution in this Order has still to be determined, and is certainly of great systematic value. D'Arbaumont has described these hairs in *Cissus antarctica*, Vent., as well as in two plants of the Paris Garden under the names *Cissus inaequilatera* and *Ampelopsis hederaefolia*. The two-armed hairs are either without a stalk or are narrowed below into a stalk, and are in both cases inserted on a group of epidermal cells; their arms, which are of equal length, either lie in the same straight line or are directed upwards so as to form an acute angle[3].

Typical glandular hairs are rare; on the branch of *Cissus gongylodes*, Burch., Jumelle observed shortly stalked external glands with a spherical head, consisting of only one cell and sometimes occurring on the apex of an emergence resembling a shaggy hair. On the other hand, in many members of the Order (*Vitis vinifera*, *V. odoratissima*, *V. Sieboldii*; *Ampelopsis quinquefolia*, *A. Veitchii*; *Cissus*

[1] J. E. Planchon, Ampelideae, in Suites au Prodrome, vol. v, 1887. In what follows, however, I do not usually take account of the generic and specific terminology of this monograph, but, in order to avoid confusion, quote the same specific names (although they may be synonyms), as are employed in the anatomical works concerned.

[2] According to Highley (The microscopic crystals contained in plants, Americ. Naturalist, Nov. 1880) the raphides of *Vitis aestivalis*, *V. cordifolia*, and *V. vinifera* consist of phosphate of lime, while the clustered crystals present in the older stem and in the berries of the species named consist of tartrate of lime. A critical examination of this and of other similar but very doubtful statements of Highley's, referring to members of other Orders, is desirable.

[3] I have not been able to find the stellate hairs stated by Blenk to occur in *Vitis oxyphylla*, Rich. (= *Cissus Schimperi*, Hochst.).

heterophylla, *C. Hochstetteri*, *C. orientalis*, *C. quadrangularis*, *C. velutina*), what are known as pearl-glands occur; they have repeatedly formed the subject of investigations (by Hofmeister, De Bary, d'Arbaumont, Kreuz, Müller-Thurgau, and Penzig). The pearl-glands are large, usually spherical structures, which are provided with a short stalk. Their internal portion consists of very large polygonal cells, and is clothed by a small-celled epidermis, which in each gland is provided with a stoma, usually found on the side opposite to the stalk, but more rarely placed laterally. The cells of the gland are rich in plastic nutritive substances (proteid, fatty oil, and sugar), and thereby indicate the biologic significance of these glands as food-bodies. The pearl-glands are deciduous structures, and do not always occur in equal quantities in the same species; e.g. in the different varieties of the vine. Their differentiation also appears to be dependent on the vigour of the plant and the humidity of the air. The external glands, occurring in *Leea aequata*, L. (Fig. 52, *B*, *C*) and examined by me in detail, are in some respects similar to the pearl-glands just described. They have a disc-like form, and therefore have the appearance of a small peltate scale, perceptible even to the naked eye; they had previously attracted the attention of Clarke[1], who mentions that these glands do not appear in any other species of *Leea* and that they consequently enable *Leea aequata* to be easily distinguished from all the other species.

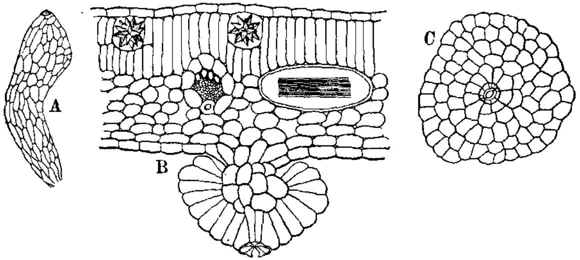

FIG. 52. A, Pearl-gland of the vine. B–C, *Leea aequata*, L.: B, Section through the leaf and through a gland; C, Surface-view of the gland.—A, after Penzig; B–C, original.

The glands in question consist, (*a*) in their central part, of a small group of approximately isodiametric and fairly small cells, which apparently represent a continuation of the leaf-parenchyma, and (*b*) of epidermal cells, which are elongated like palisade-cells, are radially inserted on the central portion, and form the greater part of the gland, which is nearly semicircular in section. Strictly speaking these characteristic epidermal cells are broadened like wedges from the central part towards the surface of the gland, as indeed the form of the gland requires. They are filled with white glistening contents, which are soluble in eau de Javelle, are not mucilaginous, and are not stained by iodine-solution or osmic acid; they combine to form the surface of the gland, each of them having a rounded-polygonal external surface. This characteristic epidermis is only interrupted at one place, namely, at that situated diametrically opposite to the point of attachment of the gland, where, as in the pearl-glands, a stoma with widely gaping pore occurs. The physiological meaning of these glands, and possibly also their relation to the pearl-glands, has still to be determined.

It remains to be added that in many cases the leaf-teeth secrete mucilage in the bud, e.g. in *Vitis vinifera*. According to Reinke, the leaf-teeth of *Vitis vinifera* do not possess a special type of structure; they only contain raphide-cells with abundant mucilage, and the termination of a vascular bundle, and they have a few stomata on the upper side.

[1] A Revision of the Indian species of *Leea*, Journal of Botany, 1881, p. 164.

3. STRUCTURE OF THE AXIS. We are much better acquainted with the ucture of the axis in this Order than with that of the leaf; the former has ɜn investigated especially by d'Arbaumont[1].

In a transverse section of the axis one is especially struck by the wide lumina the vessels, which, according to H. Schenck, in *Cissus sulcicaulis*, Planch., .ain the greatest diameter (·48–·58 mm.) that occurs in any liane, and next the broad primary medullary rays and in older stems also by the broad ɔondary medullary rays which more or less distinctly split up the xylem-mass to lamellae in the same manner as in *Clematis* and *Aristolochia*. As in *Clematis* e medullary rays are traversed by connecting strands of tracheae.

The groundwork of the **wood** varies in appearance. In many cases the ɑole of the xylem-tissue (including the medullary rays) is lignified. In other embers of the Order, on the contrary (especially the species of *Cissus* with soft ems), the outer parts of the medullary rays retain their thin walls and remain ılignified, or the whole of the groundwork of the wood consists of unlignified arenchymatous tissue with thin walls, in which the vessels are embedded in roups, each group surrounded by a sheath, consisting of a little lignified wood-arenchyma and wood-prosenchyma. According to H. Schenck, the structure ıst described occurs, for example, in *Cissus Selloana* (Bak.) Planch., *C. sulcicaulis* Bak.) Planch., *C. meliaefolia*, Planch., and *C. sicyoides*, L.; according to d'Arbau-ɑont, especially in *C. mollis*, Steud. and *C. quadrangularis*, L.; according to ..icopoli, in *C. acida*, L. Not uncommonly subsequent dilatation takes place n the unlignified tissue of the medullary rays, as well as in the unlignified vood-parenchyma of the stems last referred to.

The following statements may be made regarding the individual elements ɔf the wood. The vessels as a rule have simple circular or elliptical perfora-:ions; side by side with these I was also able to demonstrate scalariform ɔerforations in the neighbourhood of the primary wood of *Leea aequata*, L., as Sanio observed in *Vitis vinifera*. Where the vessels touch one another scalariform bordered pits are found in *Vitis vinifera*, in *Leea aequata*, and according to d'Arbaumont, in many other but by no means in all members of the Order; where ray-parenchyma adjoins the vessels I observed simple pitting on the vessel-wall both in *Vitis vinifera* and in *Leea aequata*. The wood-parenchyma is generally (apart from the soft-wooded species of *Cissus* mentioned above) restricted to the neighbourhood of the vessels. The wood-prosenchyma bears simple pits, and the lumina of the fibres are usually septate owing to a few thin division-walls. Besides the simple-pitted wood-prosenchyma tracheides are sometimes present; they are provided with scalariform bordered pits and in addition are often spirally thickened.

The **pith** has also been submitted to accurate investigation by d'Arbaumont. Among his results we may briefly mention that the cells of the pith have walls of varied thickness, and that both heterogeneous and homogeneous pith occur.

With regard to the structure of the **cortex** the periderm-formation may first be mentioned. Certain species, e.g. *Parthenocissus* (*Ampelopsis*) *quinquefolia*, Planch., form periderm very early, immediately below the epidermis, and renew it from the same phellogen for many years (perhaps even as long as the plant lives) after each year's production has been bounded by a layer of sclerotic cork. In some species, on the other hand, e.g. in *Vitis vinifera*, the first periderm arises on the inner side of the primary bundles of bast-fibres, and in the succeeding years ring-bark is formed; the cork-cells in this case usually have

[1] Unfortunately the plants investigated are described by d'Arbaumont in such an unsystemati and even incorrect manner, that a more detailed account of the results obtained cannot b given here.

thin walls and only solitary cells are sclerotic. Considered from the systematic stand-point, the second type (internal cork-formation), according to d'Arbaumont, belongs to certain species of *Vitis*, which are rather closely related to one another and are termed by him *Vites verae*[1]. In other species of *Vitis*, and also in all species of *Leea*, as well as in *Cissus*, superficial cork-formation, as first described, is present.

In connexion with the cork we may refer to the lenticels, which d'Arbaumont has examined in detail in *Ampelopsis quinquefolia*. They arise below a group of stomata, at the centre of which a specially large stoma is situated.

The primary cortex in the '*Vites verae*' has unusually thin walls and is not collenchymatous. In other species a closed (*Ampelopsis quinquefolia*) or interrupted layer of collenchyma is present. Stone-cells are absent. The occurrence of perforations in cells of the primary cortex of *Cissus antarctica*, Vent., is extremely remarkable (d'Arbaumont).

The pericycle varies in its nature. In some members of the Order, e. g. in the '*Vites verae*' of d'Arbaumont, isolated groups of bast-fibres are found at the outer limit of the bast. Between these, isolated stone-cells occasionally occur, so that a transition is afforded to the composite and continuous ring of sclerenchyma, which has been observed, e. g. in *Cissus capensis*, Willd. The primary bast-fibres of *Vitis vinifera*, &c., which are short-lived in consequence of the internal development of cork (see above) occurring in these species, have unusually wide lumina and comparatively thin walls, being at the same time septate owing to thin division-walls ; those of *Ampelopsis quinquefolia* become strongly thickened and sheathed by chambered fibres, which contain solitary crystals. Secondary hard bast is present in the '*Vites verae*.' It sometimes causes (e. g. in *Vitis vinifera*) distinct stratification of the bast. The secondary hard bast-fibres of *Vitis vinifera*, which are described by Möller as sclerotic parenchyma, differ essentially from the primary hard bast-fibres ; they are shorter, more abundantly pitted, and are quadrangular in cross-section, but they too are of the nature of fibres, have fairly wide lumina, and are (like the primary fibres) septate by means of one or two thin cross-walls. With regard to the elements of the soft bast, it is worthy of note that in *Vitis vinifera* the portions of soft bast separated by the medullary rays are placed in connexion with one another by strands of sieve-tubes, which traverse the medullary rays transversely (Wilhelm).

Oxalate of lime is present in the axis in the form of solitary crystals, clustered crystals, raphides and small acicular crystals ; the latter, which, according to d'Arbaumont, are present in the primary cortex and soft bast of numerous members of the Order (e. g. *Ampelopsis dissecta*, *Cissus angulata*, Lam., *C. papillosa*, Bl., &c.), are essentially distinguished from the raphides by their shortness and by the fact that they are not embedded in mucilage. In connexion with the crystalline elements of oxalate of lime, mention may be made of the peculiar bodies, which d'Arbaumont met with in many species, and the chemical substance of which he designates cissose. The sphaerocrystals, which are developed in alcohol-material of the species of *Cissus*, appear to consist of the same substance.

So far only the normally constructed stems have been discussed. According to Schenck, **anomalous structure of the axis** is known only in a single genus, *Tetrastigma*, and in the first place in *T. scariosum*, Planch. It is of a unique type. The stem of *T. scariosum* is strap-shaped, and at first, according to Schenck, whose words I quote below, grows in thickness in a normal

[1] To these d'Arbaumont refers : *Vitis aestivalis*, Michx., *V. amurensis*, Rupr., *V. canescens*, *V. cebennensis*, *V. coriacea*, Shuttl., *V. flexuosa*, Thunb., *V. Labrusca*, L., *V. monticola*, Buckl., *V. parvifolia*, Roxb., *V. riparia*, Michx., *V. silvestris*, *V. vinifera*, L., *V. virginiana*.

anner to a breadth of 1 cm. 'As in the soft wood of the Brazilian *Cissus*-ems, broad parenchymatous primary medullary rays separate the individual ates of wood and bast, which on the narrow sides of the stem have an accele-ted growth. In each strip of wood and bast on the narrow side, a narrow strip cambium is then newly formed from phloem-parenchyma, immediately side the first-formed strand of soft bast, which is covered externally by a rimary bundle of sclerenchyma. By the activity of the newly formed strip f cambium a new strip of wood and bast becomes intercalated in the prolonga-ion of the existing tissues.' Gilg has also met with the same anomaly in other pecies of this genus (from New Guinea).

Literature: Hofmeister, Allg. Morph. d. G., 1868, p. 545.—Licopoli, Strutt. del fusto della *Visteria chinensis* e del *Cissus acida*, Napoli, 1872, Tav. Fig. 5–8.—Reinke, Pringsheim Jahrb., Bd. x, 876, p. 158.—Möller, Denkschr. Wiener Akad., 1876, pp. 66 and 362.—De Bary, Vergl. Anat., 1877.—Penzig, Anat. e morf. della vite, Archiv. del Laborat. crittogam. di Pavia, vol. iv, 1878, p. 18.—D'Arbaumont, Stomates et lenticelles du *Cissus*, Bull. Soc. bot. de France, 1877, pp. 18 and 48 et seq.—Kreuz, Sitz.-Ber. Wiener Akad., Bd. lxxxii, Abt. 2, 1881.—D'Arbaumont, Tige des A., Ann. sc. nat., sér. 6, t. xi, 1881, pp. 186–255, pl. 11–14.—Möller, Rindenanat., 1882, pp. 207–10.—Cuboni, Anat. e fisiol. delle foglie delle vite, Rivista d'enol. e viticolt. di Conegliano, ser. 2, Anno vii.—Blenk, Flora, 1884, p. 360 et seq., separate copy, pp. 73–9.—Solereder, Holzstr., 1885, pp. 101, 102.—Eiselen, Rhaphiden, Diss., Halle a. S., 1888, p. 11.—Ryder, Hypertroph. hairs on *Ampelopsis*, Proc. Ac. of Nat. Sc. of Philadelphia, 1889, part ii, p. 155.—Douliot, Ann. sc. nat., sér. 7, t. x, 1889, p. 359.—Baccalà, Anat. della *Vitis vinifera*, Lanciano, 1889, 31 pp. con 2 tav.—Müller-Thurgau, Perldrüsen, Weinbau u. Weinhandel, Jahrg. viii, 1890, n. 20, pp. 178, 179.—Strasburger, Bau u. Verr., 1891, pp. 239–56.—H. Schenck, Anat. d. Lianen, 1893, pp. 137–41 and Tab. vii.—Penzig, Perldrüsen, Congressber. Genua, 1893, p. 237 et seq. and Tab.—Walliczek, Pringsheim Jahrb., Bd. xxv, 1893, p. 214.—Mangin, Thylles gommeuses dans le vigne, Compt. rend., t. cxix, 1895, pp. 514–16.—Gilg, in Natürl. Pflanzenfam., 3. Teil, Abt. 5, 1896, pp. 433–5.—Rathay, Austr. von Gummi in der Rebe, &c., Jahresber. u. Progr. d. k. k. önol. u. pomol. Lehranst. in Klosterneuburg, Wien, 1896, separate copy, p. 10 et seq.—Jumelle, Ét. anat. du *Cissus gongylodes*, Revue gén. de bot., n. 100, 1897, pp. 129–49.—[Kalberlah, Bau von *Tetrastigma*, Zeitschr. f. Naturw., Bd. 71, 1898, pp. 161–218.]

SAPINDACEAE.

1. Review of the Anatomical Features. The following features are specially characteristic and are of importance in distinguishing a member of Sapindaceae from allied Orders, or at any rate from Orders which are similar to the Sapindaceae in habit: on the one hand, the composite and continuous ring of sclerenchyma in the pericycle (exceptions: *Valenzuelia* and *Xanthoceras*), the simple perforations of the vessels, the bordered pitting of the vessels, even where they are in contact with parenchyma, the simple-pitted wood-prosenchyma as well as the anomalous stem-structure occurring in not a few members of the Order, and, on the other hand, the frequent occurrence both of secretory cell and of small external glands; lastly, the presence of saponin. In nearly all case the formation of cork is superficial; it is internal in *Dodonaea* and *Distichostemo* only. As a rule, the stomata are irregularly surrounded by several epiderm cells; in *Harpullia* and *Conchopetalum* alone do subsidiary cells occur, whic lie parallel to the pore. Oxalate of lime is usually present in the form solitary and clustered crystals; crystal-sand has been observed in the epiderm of the leaf of *Exothea*; styloids have been found in the bast of *Diatenoptery* The following are special anatomical features, which have been observ in this Order and are important for detailed diagnosis: the frequent gelati zation of the epidermis of the leaf, the papillose differentiation of the low epidermis, the occurrence of thin vertical or horizontal division-walls in t epidermal cells of the leaf, the occurrence of hypoderm below the upper epiderm and of sclerenchyma-fibres in the mesophyll, the varied nature of the cloth and glandular hairs—(among the former: (*a*) simple unicellular trichomes w ... differentiation as two-armed hairs, and (*b*) tufted hairs; am

the latter: small peltate scales)—&c. As regards the anomalies in the stem-structure the following types occur: (*a*) a compound xylem-mass in species of *Serjania* and *Paullinia*; (*b*) a divided xylem-mass in a few species of *Serjania*; (*c*) a reticulate xylem-mass in species of *Paullinia*, *Serjania*, and *Thinouia*; (*d*) a grooved xylem-mass, which subsequently becomes split up, in species of *Urvillea* and *Serjania*.

2. STRUCTURE OF THE LEAF. The structure of the leaf as also that of the axis has been submitted to a thorough investigation by Radlkofer, who monographed the Order; in the following pages the results of his investigations are given, based on his descriptions in the 'Sitzungsberichte der Münchener Akademie, 1890,' and in Engler's 'Natürliche Pflanzenfamilien[1].'

The **epidermal cells** of the leaf are either polygonal or undulated, and are often provided with pits in the bays of the undulations, more rarely on the whole of the external wall. Epidermal cells with undulated walls and with pits in the bays of the undulations occur (especially on the upper side) either in all or only in certain species of the genera *Atalaya*, *Chytranthus*, *Pancovia*, *Lychnodiscus*, *Melanodiscus*, *Talisia*, *Lecaniodiscus*, *Haplocoelum*, *Euphoria*, *Xerospermum*, *Alectryon*, *Matayba*, *Laccodiscus*, *Aporrhiza*, *Blighia*, *Eriocoelum*, *Phialodiscus*, *Guioa*, *Cupaniopsis*, *Lepiderema*, *Storthocalyx*, *Sarcopteryx*, *Trigonachras*, *Toechima*, *Synima*, *Sarcotoechia*, *Arytera*, *Mischocarpus*, *Lepidopetalum*, *Exothea*, *Doratoxylon*, *Harpullia*. The thick-walled epidermal cells on the lower side of the leaf in the three species of sections I and II of *Otophora* have pits on the whole of the external wall; similar pits are also found, especially on the upper side, in *Placodiscus* and some species of *Matayba*, *Elattostachys*, and *Arytera*. Numerous sclerosed epidermal cells have been observed in *Matayba purgans*. Other special features of the epidermis of the leaf depend on the height of the epidermal cells, which is considerable in *Otophora*, *Deinbollia*, and *Sarcopteryx*; the occurrence of delicate secondary vertical walls in the epidermal cells of species of *Macphersonia*, *Euphoria*, *Xerospermum* (section II), species of *Alectryon*, *Heterodendron*, species of *Tina*, *Cupaniopsis*, and *Arytera*; and the occurrence of division-walls parallel to the surface of the leaf in *Cupaniopsis* and *Gongrodiscus*. Gelatinization of the epidermis of the leaf, or of the inner walls of the epidermal cells is a wide-spread phenomenon; not uncommonly this takes place to such an extent that the cells concerned displace the chlorophyll-bearing tissue, and are clearly seen in the dry leaf as transparent dots. The mucilaginous epidermal cells are present either in all or only in some of the species of a genus, and in the latter case they are not uncommonly characteristic of a small group of closely allied species. They are wanting almost throughout in the tribe Sapindeae (with the exception of some species of *Toulicia* and *Deinbollia*), in the Lepisantheae (with the exception of *Chytranthus* and *Pancovia*), in the Melicocceae (with the exception of *Tristira* and *Tristiropsis*), in the Schleichereae (with the exception of *Schleichera*), in the Nephelieae (with the exception of *Pometia*, *Heterodendron*, *Pappea*, and species of *Nephelium* and *Alectryon*), and in the Cupanieae (with the exception of *Dilodendron*, *Tripterodendron*, *Blighia*, *Eriocoelum*, *Phialodiscus*, *Jagera*, *Trigonachras*, *Lepidopetalum*). In the genera of the remaining tribes the occurrence of these mucilaginous cells, at least in some of the species, is the rule, but with the following exceptions: *Athyana* (Thouinieae); *Erioglossum* and *Aphanococcus* (Aphanieae); *Stocksia* (Koelreuterieae); *Llagunoa* (Cossignieae); *Lixodiscus* (Dodonaeeae); *Hypelate*, *Averrhoidium*, *Hippobromus*, *Doratoxylon*, *Ganophyllum* (Doratoxyleae); *Conchopetalum* (Harpullieae). Of the genera *Serjania*, *Paullinia*, and *Allophylus*, which are the richest in species, the last-named is distin-

[1] Radlkofer's classification, to which reference will repeatedly be made below, is quoted also in Durand's Index, and hence is accessible to all.

ıished by the fact that only one or two of its species (*A. occidentalis*, *A. velu-ıus*, *A. sericeus*, and *A. inaequilaterus*) do not show gelatinization. In ›nnexion with the gelatinization of the epidermis of the leaf, it may be ıentioned that gelatinization of hypodermal cells has been observed in *hinouia obliqua* and that mucilaginous cells also occasionally (*Serjania com-unis*) occur in the interior of the leaf. Another feature not uncommon in ıe Order is the formation of papillae on the lower side of the leaf. In this case ıch cell is produced into a papilla, which, in most of the plants possessing this tructure, ends in a small jagged crown or head ; cuticular ridges usually run ownwards from the jagged prominences, are continued over the external urface of the cell, and (taking the shortest route) unite with those of the ıeighbouring cells, thus forming a very neat network. Formation of papillae ›ccurs either in all or only in certain species of a genus, specially in the tribe Nephelieae (in *Euphoria*, *Otonephelium*, *Pseudonephelium*, *Litchi*, *Nephelium*, n species of *Alectryon* and in *Podonephelium Homei*) and in the Cupanieae (in species of *Cupania* and *Guioa*, in *Dilodendron* to a slight extent and in *Stortho-calyx* and *Gongrodiscus*), and besides these in *Atalaya hemiglauca* and *A. varii-folia*, in *Plagioscyphus*, *Cotylodiscus* and *Castanospora*.

The **stomata** usually only occur on the lower side of the leaf. They are present in abundance on both sides of the leaf in some of the Serjanieae (*Serjania californica*, *S. cissoides*, *S. sphenocarpa*, *S. trichomisca*), in *Paullinia sonorensis*, in *Pappea capensis*, *Lepiderema papuana* and species of *Dodonaea*. Some species of *Serjania*, other than those mentioned, have a few stomata above the veins. As a rule the stomata are surrounded by a ring of neighbouring cells, which are not of special form or specially arranged. Special subsidiary cells, placed parallel to the pore, have been met with only in *Harpullia* and *Conchopetalum*. Among the special features of the stomata we may first mention the occurrence of very numerous and small stomata in *Toulicia*, *Porocystis*, *Sapindus*, *Talisia*, *Tristira*, *Schleichera*, in the Nephelieae and some Cupanieae (*Dilodendron*, *Molinaea*, *Guioa*, *Toechima*, *Sarcotoechia*, *Elattostachys*, *Arytera*, *Mischocarpus*, *Lepidopetalum*, *Paranephelium*), while large stomata in small numbers occur in *Aphania* and *Otophora*. The stomata generally lie in the plane of the epidermis ; stomata projecting above the surface of the leaf are present in *Paullinia subcordata*, *Cupania rubiginosa* and *Melanodiscus*, stomata sunk below the plane of the leaf-surface in *Atalaya*, *Plagioscyphus*, *Cotylodiscus*, *Pappea*, and more or less in all leaves which are characterized by formation of papillae (see above). The stomata of *Rhysotoechia* deserve special notice ; they have a wide front cavity, over which, however, a closing membrane with a narrow, round opening is stretched.

The **hypoderm**, which has been observed on the upper side of the leaf in some members of the Order, is either of a parenchymatous or of a prosenchymatous nature. Parenchymatous hypoderm has been observed in *Atalaya*, *Talisia squarrosa*, *Alectryon macrococcus*, *Cupania triquetra*, species of *Matayba*, *Mo-linaea*, *Storthocalyx*, *Elattostachys*, *Arytera*, *Harpullia* and *Conchopetalum* ; i sometimes has the same contents as the palisade-tissue, and in the species o *Cossignia* contains a rather soft, homogeneous or lamellated substance, th chemical nature of which is not known. A fibrous hypoderm in the form c a layer of fibres, spreading out from the vascular bundles of the veins, . developed in *Euphoria Gardneri* only.

The **leaf-structure** is usually bifacial, rarely centric. More or less pr nounced centric leaf-structure is found in *Paullinia sonorensis*, *Elattostach vitiensis*, completely centric structure in *Lecaniodiscus fraxinifolius*, *Heter dendron oleifolium*, *H. diversifolium*, *Koelreuteria*, *Stocksia*, *Erythrophy Diplopeltis*, *Dodonaea platyptera* and other species of *Dodonaea* as well as *Xanthoceras*. The following are special features of the mesophyll : scler

chyma-fibres occur in the leaf-tissue of certain species of *Serjania* (*S. acutidentata*, *S. ichthyoctona*, *S. obtusidentata* and *S. paucidentata*), *Paullinia stenopetala*, *Haplocoelum inopleum* and *H. trigonocarpum*, *Cupaniopsis inoplea* and *Harpullia aeruginosa*; sclerenchymatous cells in the palisade-tissue in *Matayba macrostyla* and *M. tovarensis*; the lower layers of the spongy parenchyma become sclerosed in species of *Xerospermum*, *Matayba tovarensis* and *M. longipes*. We may also mention: the occurrence of large mesh-like spaces in the spongy parenchyma in *Otophora*, *Plagioscyphus*, *Otonephelium*, *Pseudonephelium*, *Eriandrostachys*, *Paranephelium*, *Ganophyllum*, and species of *Harpullia*, and the almost complete disappearance of the intercellular spaces of the spongy parenchyma in *Talisia*, *Melicocca*, species of *Alectryon*, *Podonephelium*, *Pappea*, *Tina*, *Cupaniopsis*, *Elattostachys*, *Arytera*, *Averrhoidium*, approximately also in *Toulicia* and species of *Atalaya* with palisade-like elongation of all the cells of the mesophyll; the occurrence in the mesophyll of a middle layer, which contains tannin in *Melanodiscus*, and is differentiated in other ways in *Lecaniodiscus*, *Elattostachys vitiensis*, &c.; transverse septation of the cells of the palisade-tissue in *Eriandrostachys*, species of *Macphersonia*, in *Otonephelium*, species of *Nephelium*, *Pometia*, and *Alectryon*, in *Magonia* and *Xanthoceras*; and special form of the palisade-cells, which are hour-glass-shaped in *Lepidopetalum*, shaped like a top in species of *Harpullia*, scarcely longer than broad in *Toechima* and *Rhysotoechia*, and provided with small transverse folds in *Conchopetalum*. A fatty substance is frequently found stored in the cells of the dry leaf, especially in the assimilatory tissue.

With regard to the structure of the **veins**, among those of average size, embedded as well as vertically transcurrent veins have been observed; the latter in *Bridgesia*, *Athyana*, *Diatenopteryx*, *Thouinia*, *Thouinidium*, *Toulicia*, *Porocystis*, *Hornea*, *Plagioscyphus*, *Euphoria*, *Litchi*, *Xerospermum*, *Nephelium*, *Alectryon*, *Pappea*, *Stadmannia*, *Synima*, *Mischocarpus*, *Paranephelium*. The occurrence or absence of sclerenchyma, accompanying the vascular bundles of the veins, is important for the characterization of species.

In the **petiole** of most of the woody species a ring of sclerenchyma surrounding the principal system of vascular bundles appears to occur; occasionally medullary and cortical vascular bundles are present in the petiole besides the principal system of bundles. The herbaceous species *Cardiospermum Halicacabum* possesses four isolated vascular bundles in the petiole (Petit).

Internal **secretory elements** are present only in the form of secretory cells, which not uncommonly produce transparent dots or small striae in the dry leaf. Two forms of secretory cells are found; in many species they occur side by side, being either sharply distinguished or merging into one another; they appear in the form of (*a*) elongated, tubular secretory cells, i.e. 'secretory sacs' which run in uniseriate rows of variable length near the lower epidermis either in the neighbourhood of the vascular bundles or independently of the latter, and (*b*) 'secretory cells' which are rounded or of irregular shape, and occur in the palisade or in the spongy tissue, or at the boundary of the two. In the living plant the contents of these secretory cells no doubt always resemble latex. In herbarium-material they show varying features, being either clear and colourless or turbid and varying in colour from yellowish brown to brownish black. In like manner the contents behave in different ways towards solvents, such as water and alcohol, and occasionally form a froth with water, which leads one to infer the presence of a substance like saponin. The contents of the secretory cells of *Stocksia* and *Erythrophysa* give a tannin-reaction, while in *Paranephelium* chlorophyll-grains are present in the secretory cells. Further investigation is required to determine whether the poisonous properties of many Sapindaceae are due to the contents of the secretory cells in question. Regarding the distribution of the secretory cells and their consequent systematic value,

ntion may first be made of the fact that these elements are usually ıstant for a species, although the abundance, in which they occur, is t always constant in the same species. The secretory cells were found t to be constant in the following species only: *Urvillea ulmacea, Sapindus ponaria, S. Mucorossi, Xerospermum Noronhianum*, and *Guioa glauca.* cretory cells (including secretory sacs) have not been observed: in species of *alaya, Sapindus, Deinbollia, Hornea*; in the Aphanieae except in species of *'ioglossum* and *Aphania*; in *Lepisanthes, Chytranthus, Lychnodiscus, Placoscus, Melanodiscus, Crossonephelis*; in the Melicocceae except *Castanospora* ıd *Tristiropsis*; in the Schleichereae except *Haplocoelum*; in the Nephelieae ccept *Euphoria* and *Pappea*, species of *Xerospermum, Nephelium*, and *Pometia*; certain Cupanieae, namely in *Scyphonychium, Pseudima, Laccodiscus, porrhiza, Blighia, Eriocoelum racemosum, Phialodiscus*, species of *Guioa, upaniopsis*, and *Rhysotoechia*, in *Dictyoneura, Sarcopteryx Martyana, Jagera utifolia*, species of *Elattostachys, Arytera*, and *Lepidopetalum*; and, finally, mong the Dyssapindaceae, in *Koelreuteria, Loxodiscus, Diplopeltis* pro parte, ı species of *Dodonaea*, in *Exothea Copalillo*, in *Doratoxylon, Ganophyllum*, pecies of *Harpullia*, in *Xanthoceras* and *Ungnadia.* Lastly, the secretory :ells, when small or not characterized by special contents, are occasionally lifficult to demonstrate, and within certain genera, which, like *Serjania*, ›ossess both kinds of secretory cells only in a certain number of their species, groups of allied species are occasionally distinguished by the absence of secretory cells.

Oxalate of lime is excreted in the leaves in the form of ordinary solitary and clustered crystals, in one case (*Exothea*) of crystal-sand also. In species of *Paullinia, Chytranthus, Pancovia, Xerospermum, Pometia, Ganophyllum, Filicium*, and *Conchopetalum* crystals occur in the epidermis of the leaf, whilst crystal-sand is found there in *Exothea Copalillo.* In the mesophyll either solitary crystals alone (occasionally in the form of straight or bent rod-shaped crystals in the palisade-tissue) have been observed, or clustered crystals or both kinds. Accompanying the vascular bundles of the veins solitary crystals are usually present, more rarely (e.g. in *Cardiospermum* and *Bridgesia*) clustered crystals.

The **hairy covering** consists of clothing and glandular hairs. The former are generally bristle-like, unbranched and unicellular or provided with two or three thin cross-walls in the lower portion. A special form of these trichomes is constituted by quite short hairs, the bases of which are swollen into a spherical form, usually spirally striate, and sunk below the epidermal cells. This form of hair with striation of the basal portion is found in *Pancovia, Matayba*, and *Xerospermum* (section I, *Tetrasepalum*), and without striation in *Chytranthus.* The hairs of *Pentascyphus* also show striation of the basal wall. Another modification of the bristle-hairs occurs in *Lychnodiscus*, some Nephelieae (*Nephelium, Pometia, Alectryon, Stadmannia*) and species of *Matayba* (*M. glaberrima, M. paucijuga, M. arborescens, M. floribunda*), to which a tendency of the trichomes to become two-armed is peculiar. Lastly, multicellular tufted or stellate hairs occur in *Euphoria* (except *E. Gardneri*), *Cossignia Harpullia, Arfeuillea*, and *Xanthoceras*, in some cases besides simple hairs Glandular hairs are widely distributed and are perhaps present on youn leaves throughout the Order. The most frequent forms are small externa glands with a short, few-celled and uniseriate stalk and a small few-celle usually oval head, which is bent over. The following types require speci mention: the depressed glands of the Aphanieae except *Erioglossum*, the Sapindeae *Deinbollia, Sapindus* and *Hornea* (in the last two genera wit peculiar oblique insertion of the glands on the inner surface of small d ... Lepisantheae *Lepisanthes* and *Otophora* (with the exceptic

of *O. alata*, which has no glands), of the Cupanieae *Pseudima*, *Rhysotoechia* (except *R. flavescens*, which has no glands) and *Matayba* pro parte. The external glands show transitions to small multicellular peltate scales in *Lychnodiscus* and *Smelophyllum* among the Lepisantheae, in *Lecaniodiscus fraxinifolius* among the Schleichereae, in *Stadmannia* among the Nephelieae, in the section *Mizopetalum* of the genus *Cupaniopsis*, in *Lepiderema*, *Dictyoneura*, and the section *Azarytera* of the genus *Arytera* among the Cupanieae, and in species of *Dodonaea*, in *Ganophyllum* and *Filicium* among the Dyssapindaceae; in these the shield either exhibits radially placed ray-cells (*Arytera*) or irregularly arranged polygonal cells (*Filicium*, *Ganophyllum*, and *Smelophyllum*). In some genera the external glands are characterized by specially large size, e.g. in *Melanodiscus*, *Crossonephelis*, *Talisia*, and in the Dyssapindaceae, e.g. in *Llagunoa* and *Loxodiscus*, in which the external glands are of much more complicated structure (analogous to what are termed glandular shaggy hairs with a secretory palisade-like epidermis) and occasionally contain clustered and solitary crystals in the head of the gland; in other cases, e.g. species of *Serjania*, and in *Erioglossum* and *Podonephelium* the external glands are characterized by the head being distinctly delimited towards the stalk, and in *Paullinia obovata* by their occurrence in pairs. Lastly, those members of the Order may be mentioned in which it has not been possible so far to observe glandular hairs. These are: *Valenzuelia*; *Toulicia*, *Porocystis*; *Otophora alata*; *Chytranthus*, *Pancovia*, *Placodiscus*; *Melicocca*, *Glenniea*, *Castanospora*, *Eriandrostachys*, species of *Macphersonia*, *Tristiropsis*, *Tristira*; the Schleichereae (except *Lecaniodiscus fraxinifolius*, which has glands resembling small peltate scales); among the Cupanieae species of *Cupania*, *Matayba*, *Tina*, *Molinaea*, and *Phialodiscus*, *Storthocalyx*, *Trigonachras acuta*, species of *Toechima* and *Arytera* (excluding the species of *Azarytera* with small peltate scales); finally, several Dyssapindaceae, namely species of *Dodonaea* and *Harpullia*, *Conchopetalum* and *Xanthoceras*.

The external appearance of the dried leaf, depending on the presence of special contents in the epidermis and mesophyll, is not without systematic value. Special contents of the epidermis cause the lead-grey or yellowish green colour of the dried leaf in the Aphanieae, Lepisantheae, and some Cupanieae (*Rhysotoechia*). The chocolate-brown colour of the lower side of the leaf of *Otophora* is due to the tannin-contents of the mesophyll. The leaves of *Nephelium* and *Guioa* show a similar brown coloration, the leaves of *Elattostachys* have a blackish brown, those of *Harpullia* a blackish green colour. The young leaves of *Otophora*, *Talisia*, *Schleichera*, *Pometia*, and *Nephelium* are characterized by a red coloration (as in those of the Leguminous genus *Brownea*, which in gardens is occasionally confounded with *Talisia*). Finally, the sticky resinous coating, which covers the epidermis of the leaf and branch in many species of *Dodonaea*, in *Llagunoa glandulosa*, *Ganophyllum*, and *Filicium*, is the secretion of the external glands.

3. Structure of the Axis. The most important character of the **cortex** for the anatomical diagnosis of the Order is the occurrence of a composite and continuous ring of sclerenchyma at the outer limit of the bast. Primarily this sclerenchymatous sheath consists almost entirely of bast-fibres; subsequently groups of stone-cells insert themselves between the bast-fibres. The composite and continuous ring of sclerenchyma in question is found in all the Sapindaceae with the exception of the two monotypic genera *Valenzuelia* and *Xanthoceras*; in these, isolated primary groups of bast-fibres alone are present in the pericycle, but in their neighbourhood sclerenchyma of the nature of rod-cells occurs in *Valenzuelia*. The primary hard bast-fibres, especially those with wide lumina, occasionally show thin cross-walls in small numbers (*Cardiospermum Halicacabum*, *Serjania piscatoria*, *S. cuspidata*, &c.). Within the ring of

lerenchyma the secondary cortex of herbarium-branches possesses no condary bast-fibres or only few and small groups of them, and in their place lerosed rod-cells are occasionally found (*Eriandrostachys Chapelieri, Podonephelium Homei*). In the secondary bast of *Magonia* groups of stone-cells ccur; in other cases bands of bast-fibres, which include stone-cells. The latter i *Thouinia striata* and *Stadmannia Sideroxylon* are united into regular inner clerenchyma-rings. In the sieve-tubes both simple and scalariform sieve-lates occur. The primary cortex shows collenchymatous tissue especially n the angles of the branch in those species which climb by means of tendrils; n other cases the external portion of the primary cortical parenchyma is often lifferentiated as collenchyma. Groups of stone-cells are not uncommon in he primary cortex, e.g. in *Atalaya multiflora, Sapindus Rarak, Melicocca nijuga, Talisia pulverulenta*; in *Toulicia guianensis* band-shaped groups of hese stone-cells are fused so as almost to form a ring. The development of cork almost always takes place subepidermally or at least in one of the adjoining outer layers of the primary cortex (the latter, e.g., in species of *Otophora, Lepisanthes, Talisia, Nephelium, Stocksia*). *Dodonaea* and *Distichostemon*, however, form a noteworthy exception. Here the formation of cork begins immediately within the sclerenchyma-ring; the phellogen not only forms cork on its outer side, but also phelloderm on its inner side, and subsequently a new phellogen is formed within a second ring of sclerenchyma, which arises at the inner limit of the phelloderm; this ring of sclerenchyma, however, contains no true bast-fibres, but only rod-cells. In a similar manner the formation of a third ring of sclerenchyma takes place, and so on, followed each time by new cork-formation, so that, while the outer layers become thrown off, a multiple (2–4-fold) zone of sclerenchyma and cork is retained on the branch. The cells of the cork usually have fairly thin walls; one-sided sclerosis of the inner or outer (*Laccodiscus*) tangential walls of the cork-cells, however, occurs in various genera, and likewise (*Blighia*) thickening of all the walls in some of the cells.

The following statements may be made regarding the structure of the **wood**. The medullary rays almost throughout the Order are narrow, usually 1–2, at the most 3–4 cells broad. Even the Paullinieae with anomalous structure have no broad medullary rays; comparatively broad rays were found in places in *Serjania faveolata* and *Erioglossum rubiginosum*. The vessels mostly have a diameter of medium size (viz. ·03–·06 mm.), but in *Toulicia, Hornea, Melicocca, Tristiropsis, Pometia, Eriocoelum* and other genera, they have wider lumina (diameter = ·07–·08 mm.); vessels with still wider lumina (over 1 mm. in diameter) are found only in the Paullinieae, which, as is well known, are lianes, and constantly have very wide vessels. The vessels almost always have simple perforations; only in a few cases (*Harpullia, Lecaniodiscus cupanioides, Placodiscus turbinatus, Cotylodiscus stelechanthus*) have scalariform perforations with few bars been observed in the neighbourhood of the primary wood. The walls of the vessels, even where they are in contact with ray-parenchyma, are furnished with bordered pits. More or less distinct spiral striation of the vessel-walls is found in *Valenzuelia, Koelreuteria paniculata, Stocksia, Dodonaea multijuga*, and other species of *Dodonaea*. The wood-prosenchyma, which forms the groundwork of the wood, bears simple pits Isolated thin cross-walls occur here and there in the prosenchyma-cells o almost all the genera; septate prosenchyma-cells of this kind have not bee observed in the species of *Serjania, Paullinia*, and *Urvillea* of tribe I, in *Valenzuelia* of tribe II, in *Cossignia* (including *Melicopsidium*) and *Llagunoa* of tribe X in *Loxodiscus, Diplopeltis, Dodonaea* pro parte and *Distichostemon* of tribe XI in *Harpullia* pro parte and *Xanthoceras* of tribe XIV. With regard to th elements of the wood-prosenchyma it should be noted that a wide lumen, such is found in the lime-tree, for example, does not occur anywhere in the Order :

a consequence of this the wood of the Sapindaceae is generally characterized by hardness and firmness. The wood-prosenchyma usually possesses thick walls and lumina which are not very narrow; it has relatively wide lumina, e.g. in *Porocystis toulicioides*, *Toulicia guianensis*, and *Koelreuteria paniculata*; it has very thick walls and narrow lumina in *Dodonaea* and species of *Distichostemon*, in *Cossignia pinnata* and *Lepisanthes deficiens*. Occasionally (e.g. in *Xerospermum Noronhianum*) wood-prosenchyma with thick walls and narrow lumina is present in the same plant as the form with wide lumina; the latter then contains starch, which, however, also occurs now and then (*Erythrophysa undulata*) in the ordinary wood-prosenchyma. According to Höhnel, a tier-like arrangement of the wood-fibres and of their terminal pits (but not of the medullary rays) causes the tier-like structure of the xylem-mass of *Aphania senegalensis*. The wood-parenchyma is usually not developed in abundance. It occurs in greater amount, at the same time forming tangential bands, only in *Sapindus trifoliatus* and *S. oahuensis*, *Deinbollia pinnata*, *Hebecoccus ferrugineus*, *Lepisanthes acuminata*, and *L. deficiens*, *Melicocca bijuga*, and *Magonia pubescens*. Finally, the parenchymatous wood of *Dilodendron bipinnatum* is characterized by a kind of gummy metamorphosis, a substance resembling gum being excreted in the vessels and in canal-like cavities.

The **pith** not uncommonly contains isolated stone-cells, or groups of them. In *Molinaea cupanioides* and *M. retusa* the pith consists almost entirely of stone-cells. In species of *Toulicia*, *Guioa* and *Mischocarpus* rudimentary vascular bundles, or bundles consisting of fibres only, are met with in the pith.

The **secretory organs** and the features presented by the crystals in the axis still require a more detailed description. The secretory cells are more difficult to demonstrate than in the leaf. They may occur in the primary and secondary cortex as well as in the pith. In certain genera secretory cells are found only in some of these tissues, e.g. in *Valenzuelia* and *Stocksia* in the primary cortex only; in other cases they occur in all these tissues, e.g. in certain species of *Thouinia* and *Cupania*. In most cases the secretory cells are elongated in the vertical direction, especially those situated in the bast. Shorter secretory cells are specially peculiar to the pith and primary cortex. The lumina of the secretory cells are frequently of considerable size, especially in the case of the secretory cells of the bast and primary cortex, while those of the pith are generally small. As examples of secretory cells with wide lumina, those situated in the primary cortex of *Plagioscyphus cauliflorus* with a diameter of ·108 mm. or more may be mentioned, as well as the secretory cells of the bast of *Synima Cordierii* with the relatively considerable diameter of ·036 mm. In a transverse section of the branch the secretory cells of the primary cortex and of the pith are usually isolated, while those of the secondary cortex frequently form groups, e.g. in *Jagera pseudorhus*, *Pometia tomentosa*, *Thinouia myriantha*. The secretory cells of the primary cortex in particular are arranged in longitudinal series (e.g. in *Toulicia megalocarpa*, *Plagioscyphus cauliflorus*, *Zollingeria macrocarpa*, *Tristiropsis acutangula*, *Haplocoelum inopleum*, *Xerospermum Noronhianum*, *Cupania americana*, and in others), more rarely also those of the pith (*Allophyllus Cobbe*) and of the bast (*Valenzuelia*, *Zollingeria macrocarpa*, *Castanospora Alphandi*, &c.). In the primary cortex, in the pith, and likewise in the bast of *Valenzuelia* these longitudinal series are many-celled while in the bast of the species of *Castanospora* and *Zollingeria* mentioned they are generally only few-celled (2-celled). The arrangement of the secretory cells in *Stocksia* requires special mention. These elements here form multiseriate strands, which lie a few layers below the epidermis, run in the vertical direction, and may be recognized with the naked eye as raised lines

on the surface of the branch; the secretory cells themselves have wide lumina and their contents are gummy.

Oxalate of lime is deposited in the axis, as in the leaf, in the form of clustered and ordinary solitary crystals. Styloid-like crystals have been observed only in one case, namely in the bast of *Diatenopteryx*. Exclusive occurrence of clustered crystals is not found in the axis of any member of the Order. The chambered fibres of the bast usually contain solitary crystals, rarely clustered crystals (e.g. in *Koelreuteria paniculata*, *Sapindus oahuensis*, *Erythrophysa undulata*). In the wood, chambered fibres with solitary crystals are the only type found.

The lianes among the Sapindaceae are in part characterized by an **anomalous structure** of the branch. This has been investigated in recent times chiefly by Radlkofer, Nägeli and H. Schenck, and by the first-named author specially with regard to its systematic value. Radlkofer has distinguished the different anomalies, present in the Order, under the terms compound, divided, corded, and cleft xylem-masses ('zusammengesetzte, geteilte, umstrickte und zerklüftete Holzkörper'); to which the less important anomaly, presented by a lobed xylem-mass, may be added. The compound xylem-mass (Fig. 53, *A*) depends on a special arrangement of the vascular bundles at their origin. A central ring of vascular bundles occupies the middle of the branch or stem, and, around it and separated from it by a small amount of cortical parenchyma, several peripheral rings of vascular bundles are situated. The number of the peripheral bundle-rings usually amounts to three, and each of these may be replaced by two bundle-rings lying immediately side by side; there are rarely less than three; in certain species there are about 8–10, which are placed closely side by side. The central and likewise the peripheral bundle-ring each possess a pith and, bounding the latter, primary spiral vessels (the spiral thickening of which can be unrolled). The vascular bundles of the central and of the peripheral rings are in connexion with one another at the node, the leaf-traces at first running in the central ring and subsequently passing into one of the peripheral bundle-rings. Both central and peripheral bundle-rings possess permanent growth in thickness by means of a ring of cambium proper to them, and in this way the cable-like structure of the stem originates, and is of benefit to the plant, when exposed to stretching and torsion. The compound xylem-mass, which besides occurring in the Sapindaceae has only been demonstrated in a plant, probably belonging to the Leguminosae (q.v.), is found in certain species of *Serjania* (91 out of 172) and *Paullinia* (16 out of 122). The second anomaly, the divided xylem-mass (Fig. 53, *B*), is, like the first, due to a special arrangement of the vascular bundles at their origin, and is distinguished by the fact that no central xylem-mass is formed and that the piths of the 5–7 bundle-rings (which lie side by side in a circle, and only become closed rather late on their inner sides) are at first in connexion with a central pith. The second anomaly occurs only in three species, viz. *S. corrugata*, Radlk., and allied species. The third anomaly is the corded xylem-mass (Fig. 53, *C–E*). The stems are at first normal, and grow in thickness in the normal manner up to the fifth or sixth year. Then, however, while normal growth in thickness still continues, new strands of cambium arise in the cortical parenchyma on the inner side of the sclerenchyma-ring, and become transformed into new secondary rings of wood and bast, which enclose a pith-like tissue at the centre, but possess no spiral-vessels with thickenings that can be unrolled. These secondary rings of wood and bast are in connexion with one another, but not with the original xylem-mass. A corded xylem-mass is probably present in all the species of the genus *Thinouia* and in a few species of *Paullinia*; not uncommonly it also occurs as a secondary complication in the older stems of those species of *Paullinia* and *Serjania* which possess a compound or divided xylem-mass. The

secondary masses of wood and bast are either cylindrical (*Thinouia*) or flattened in the tangential direction (*Paullinia*). The fourth anomaly, the cleft xylem-mass (Fig. 53, *F–G*) which occurs in species of *Urvillea* and in *Serjania piscatoria*, is, like the third one, a secondary phenomenon. The branch is at first normal and is only superficially grooved, owing to certain portions of the cortex being rather strongly depressed. The axis subsequently becomes split into three or more portions corresponding to the grooves, owing to the appearance of cambial tissue at these points. The separate portions of the stem then grow in thickness through the activity of a cambium, which surrounds each of them on all sides. Lastly, a lobed xylem-mass originates by increased

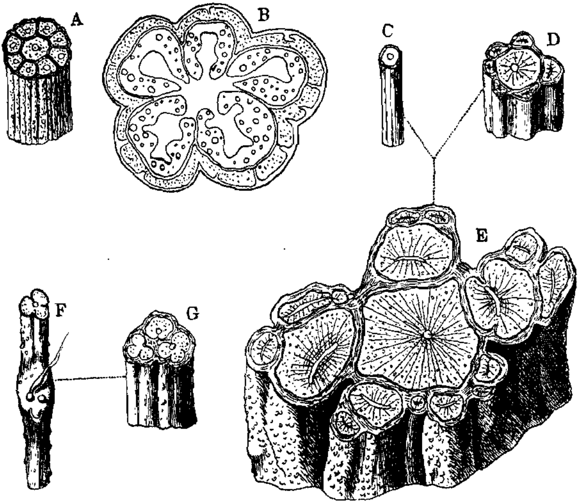

FIG. 53. A, Compound xylem-mass of *Serjania fuscifolia*, Radlk. B, Divided xylem-mass of *Serjania corrugata*, Radlk. C–E, Corded xylem-mass of *Thinouia ventricosa*, Radlk. and other species at three successive stages representing different ages. F–G, Cleft xylem-mass of *Urvillea laevis*, Radlk. at two stages in the growth.—After Radlkofer.

development of the wood at five or more places in the circumference of the stem; five or more ribs are formed, which even project externally, and are separated from one another by narrow grooves. This structure occurs in some species of *Serjania* and *Urvillea*.

NOTE.—Very little is known as to the growth in thickness of the root in those members of the Order which have a stem with anomalous structure. Crüger (Bot. Zeitung, 1851, p. 487) alone points out that those species which exhibit a compound xylem-mass in their stems do not possess it in their roots.

It may further be mentioned that the 'réseau de soutien' (cf. Cruciferae), which was discovered by Van Tieghem, is met with in a large number of cases

(species of *Sapindus, Koelreuteria, Nephelium, Talisia, Cupania*, and *Melicocca*) in the subepidermal cell-layer of the root.

Literature: Radlkofer, Struct. pecul. of certain Sapind. pl., Rep. Brit. Assoc. 1868, pp. 109–11. Varii tipi delle anomalie, etc., Atti del Congresso ten. a Firenze 1874 (impr. 1875), pp. 60–5. Monogr. *Serjania*, München, 1875; Entsteh. der sek. Holzk. etc., Ber. Naturforschervers. München, 1877, pp. 194–7; S. Holländ.-Indiens, Actes du Congrès tenu à Amsterdam, 1877; *Sapindus*, Sitz.-Ber. Münch. Akad., 1878, pp. 221 et seq.; *Cupania*, loc. cit., 1879, pp. 457 et seq.; *Serjania*, Suppl., Abh. Münch. Akad., 1886, especially pp. 2–44 and Tab. i–vii: see here also the older literature on the anomalous structure of the axis; Durchs. Punkte, in Sitz.-Ber. Münch. Akad., 1886, p. 315; Glied. d. S., loc. cit., 1890, especially pp. 303–30; Sopra il fusto anomalo delle *Serjania piscatoria*, Congressber. von Genua, 1892 (impr. 1893), pp. 66–8; Monogr. *Paullinia*, München, 1895, especially pp. 23–36; S., in Natürl. Pflanzenfam., 3. Teil, Abt. 5, 1895, pp. 281–7.—Nägeli, Dickenwachst. d. *Steng. etc. bei den S., Beitr. z. wiss. Bot., Heft 4, Leipzig, 1868*.—De Bary, Vergl. Anat., 1877.—C. de Candolle, Mém. Soc. phys. et nat., t. xxvi, 2, 1879, pp. 437 et seq.—Möller, Rindenanat., 1882 pp. 274, 275.—Höhnel, Sitz.-Ber. Wiener Akad., Bd. lxxxix, Abt. 1, 1884, pp. 43, 44.—Solereder Holzstr., 1885, pp. 103–5.—O. Bachmann, Schildh., Flora, 1886, separate copy, pp. 35, 36.—Petit Pétiole, Act. Soc. Linn. de Bordeaux, t. xliii, 1889, p. 28 and pl. i.—H. Schenck, Anat. d. Lianen. 1893, pp. 80–110, p. 253, and Tab. iii–v.—[Schwabach, Bot. Centralbl., 1898, iv, p. 357.]

HIPPOCASTANACEAE.

This small Order, consisting of the two genera *Aesculus* and *Billia*, is characterized by the lack of a special type of stomatal apparatus, by the predominance of simple perforations in the vessels, by the narrow medullary rays of the xylem and the simple pitting of the wood-prosenchyma, by the superficial development of the cork, and by the composite and continuous ring of sclerenchyma in the pericycle. The Hippocastanaceae share the above features, as also the frequent occurrence of secretory cells, with many members of the allied Order Sapindaceae. The hairy covering is formed by ordinary clothing hairs and by small external glands. Oxalate of lime occurs in the form of ordinary solitary and clustered crystals.

The **leaves**, which have been examined[1], have bifacial structure. The stomata occur only on the lower side. The epidermal cells of the leaf have undulated lateral walls and frequently a striated cuticle. In *Billia Hippocastanum*, Peyr. the epidermal cells of the upper side of the leaf are divided by thin vertical walls. Gelatinization of the epidermis of the leaves has not been observed. The smaller veins are vertically transcurrent in *Aesculus*, owing to the presence of tissue, which has thin walls, or is lignified and then occasionally has thick walls; in *Billia*, on the other hand, the vascular bundles of the smaller veins are surrounded by a ring of sclerenchyma, and are embedded in the mesophyll. In *Billia Hippocastanum*, Peyr., and *B. columbiana*, Planch. et Lind. the mesophyll is traversed by sclerenchyma-fibres, which have an irregular course. The secretory cells mentioned above are not found in the leaf in all the species. In *Aesculus turbinata*, Bl., and *A. Hippocastanum*, L.: the mesophyll contains spherical secretory cells, the membranes of which look as though they were suberized; in *A. rubicunda*, Lodd., the secretory cells are enlarged cells of the palisade-tissue; in other species of *Aesculus* (e.g. *A. parviflora*, Walt.) they appear to be absent. In *Billia Hippocastanum* and *B. columbiana*, secretory cells with wide lumina have only been observed in the bast of the veins of the leaf. Oxalate of lime is present in the leaf in the form of solitary and clustered crystals. The hairy covering consists of simple, unicellular or uniseriate clothing hairs, the surface of which is frequently finely striated, and of small external glands, similar in structure to those

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[1] The statements that follow are based principally on a casual investigation of my own of the leaves of *Aesculus Hippocastanum*, L., *A. turbinata*, Bl., and other species, as well as of *Billia columbiana*, Planch. et Lindl., and *B. Hippocastanum*, Peyr.

of the Sapindaceae. The glands which occur in *Aesculus* on the scale-leaves of the buds, and cover them with a layer of a sticky glue-like consistency, are, according to Hanstein, oblate-spherical structures, which are attached to the epidermis by a small, few-celled stalk and consist essentially of elongated papillose cells, diverging from one another like a fan; they accumulate such abundant secretion in a subcuticular position that the cuticle finally bursts.

According to C. de Candolle, the transverse section of the **petiole** exhibits an annular closed bundle-system, in the pith of which vascular bundles occur in some of the species ('*Aesculus Hippocastanum*, L., *A. rubicunda*, Herb. amat., *A. Lyoni*, hort. Kew., *A. pubescens*, hort. Kew.; *Pavia rubra*, Lam., *P. discolor*, hort. Kew.'), but are wanting in other species ('*Aesculus californica*, *A. punduana*, Wall., *A. indica*, Colebr., *A. ohioensis*, Michx., *A. chinensis*, Bunge; *Pavia macrostachya*, Herb. amat., *P. hybrida*, DC., *P. flava*, DC., *P. sibirica*, hort. Kew., *P. indica*, hort. Kew.').

The following points may be mentioned with regard to the structure of the axis, which I have investigated in *Aesculus Hippocastanum*, L., *A. parviflora*, Walt., *A. turbinata*, Bl., *Billia columbiana*, Planch. et Lindl., and *B. Hippocastanum*, Peyr. A transverse section of the **wood** shows narrow, 1–2-seriate medullary rays, vessels with rather narrow lumina (diameter = ·04 to ·05 mm.), frequently arranged radially, and wood-prosenchyma with relatively wide lumina, and with walls occasionally strengthened by the occurrence of a gelatinous layer. The perforations of the vessels are usually simple and circular or elliptical; in *Aesculus Hippocastanum* and in the two species of *Billia* scalariform perforations with fairly numerous bars occur side by side with those of the simple type. Closely placed bordered pits (the border of which has a diameter of ·003 mm.) are present on the walls with which the vessels touch one another; the vessel-wall, where it is in contact with parenchyma of the medullary rays, bears simple and bordered pits of varied size. Moreover, the pitted vessels of *Aesculus turbinata*, *A. Hippocastanum*, and *Billia Hippocastanum* are characterized by spiral thickening of their walls. The parenchyma is usually (*Aesculus*) developed to a subordinate extent, but is somewhat more abundant in *Billia*, in which chambered parenchyma, containing crystals, also occurs in the wood.

The **cortex**, as has already been pointed out above, is characterized by the superficial (subepidermal) origin of the cork and by the composite and continuous ring of sclerenchyma in the pericycle. The cork-cells are frequently sclerosed on their inner tangential walls. Stone-cells are sometimes present in the primary cortex (*Billia columbiana*, *Aesculus Hippocastanum*). Secondary hard bast, accompanied by stone-cells, has been observed by Möller in the older axes of *Aesculus*. Oxalate of lime occurs in the axis in the form of solitary and clustered crystals. Secretory cells have been found, with certainty, only in the two species of *Billia*, where they occur in the outermost part of the bast.

Literature: Hanstein, Bot. Zeit. 1868, p. 721.—Möller, Denkschr. Wiener Akad., 1876, p. 385.—De Bary, Vergl. Anat., 1877.—C. de Candolle, Mém. Soc. phys. et nat. de Genève, t. xxvi, 2, 1879, pp. 437–8, 460 and pl. i.—Möller, Rindenanat., 1882, pp. 275–8.—Solereder, Holzstr., 1885, p. 103.—Petit, Pétiole, Act. Soc. Linn. de Bordeaux, t. xliii, 1889, p. 29 and pl. i.—Brandza, Struct. de l'hybride entre l'*Aesc. rubicunda* et le *Pavia flava*, Revue de bot., ii, 1890, pp. 301–5.—Radlkofer, Glied. d. Sapindac., Sitz.-Ber. Münch. Akad., 1890.—J. E. Weiss, Denkschr. Regensb. bot. Gesellsch., 1890, separate copy, p. 65.—Ross, Malpighia, iv, 1890–1, p. 92.—Strasburger, Bau u. Verricht., Jena, 1891, pp. 213–15.—Pax, in Natürl. Pflanzenfam., 3. Teil, Abt. 5, 1893, p. 273.—Kuhla, Phelloderm, Bot. Centralbl., 1897, p. 198.

ACERACEAE.

1. Review of the Anatomical Features. The following points are haracteristic of the Order Aceraceae [1]: the lack of a special type of stomatal pparatus, the simple perforations of the xylem-vessels, which do not possess ride lumina, the simple pits of the wood-prosenchyma, the slight developnent of the wood-parenchyma, and the superficial, or at any rate never ericyclic, origin of the cork. The smaller veins of the leaf are more or less istinctly vertically transcurrent. The pericycle is of varied nature, including ither a composite ring of sclerenchyma or isolated groups of bast-fibres. *ecretory sacs with milky contents (frequently incorrectly termed laticiferous* essels in the literature) occur in certain species of *Acer* and in *Dipteronia* 1 the bast of the axis as well as in that of the leaf-veins, or very rarely *4cer campestre*, L.) also free in the mesophyll. Oxalate of lime is generally eposited in the form of ordinary solitary and clustered crystals. The hairy overing consists of simple unicellular hairs, of two-armed hairs, provided ith a uniseriate and few-celled stalk (*Acer distylum*, Sieb. et Zucc.), and of nall multicellular glandular hairs of varied structure. Amongst special atures, which are available for the diagnosis of species, the following have been bserved: mucilaginous epidermal cells in the leaf of species of *Acer* and papilse differentiation of the lower epidermis of the leaf (*Acer Pseudoplatanus*, L.).

2. Structure of the Leaf. The following description of the structure f leaf and axis is based on my own investigations of certain species of *Acer* elonging to various sections (*A. distylum*, S. et Z., *A. platanoides*, L., *A. campestre*, L., *A. Pseudoplatanus*, L., *A. Negundo*, L., and *A. spicatum*, Lam. var. *kurundense*, Maxim.).

The **leaf-structure** is bifacial in all except *A. Negundo*, the leaf of which is ntric. The stomata in all cases occur only on the lower side of the af, and are surrounded by a considerable number of ordinary epidermal lls. Epidermal cells with mucilaginous inner membranes have been observed *A. distylum*, *A. platanoides*, *A. campestre*, and *A. Pseudoplatanus*. Papillose fferentiation of the lower epidermis occurs in *A. Pseudoplatanus*. In all ecies (except *A. distylum*) the larger veins contain sclerenchyma, accompanying le vascular bundles; the small veins are more or less distinctly vertically anscurrent.

Oxalate of lime occurs in the form of clustered or solitary crystals, or both. 1 *A. Negundo* enlarged cells, occupied by a single large crystal embedded in anulated contents, occur in the mesophyll; these cells cause transparent ots in the fresh leaf. Zimmermann has observed crystalloids in the chloroasts of the palisade-tissue in *A. platanoides*. I have only met with the **cretory sacs** mentioned above in the leaf of *A. platanoides*, *A. campestre*, d *A. distylum*, the leaves of which emit a milky juice, when the living plant injured. In all three species they occur in the bast of the larger veins, and so free in the mesophyll in *A. campestre*. Only the latter will be mentioned re, as those situated in the bast also occur in the axis, and will be discussed ter on. The secretory sacs in the mesophyll of *A. campestre* are of medium ngth and varied shape; they are distinguished from the surrounding cells their wide lumen and by their contents; they are situated immediately low the one-layered palisade-tissue, in some cases also immediately above e lower epidermis; they occur either singly or united into series.

[1] The genus *Dobinea*, quoted in Durand's Index among the Aceraceae next to *Acer* and *Negundo*, s been transferred by Radlkofer, as is well known, to the Anacardiaceae (q.v.). To make up for s loss the Order has been increased by the addition of the genus *Dipteronia* established by Oliver Hooker's Icones, Tab. 1898, anno 1889); this requires mention here, as the anatomy of this nus will be discussed in the following description.

The **hairy covering** consists of multicellular glandular hairs (all species except *A. distylum*), ordinary unicellular trichomes (*A. campestre, A. Pseudoplatanus, A. Negundo,* and *A. spicatum*), and two-armed hairs with a short 2–3-celled stalk and a horizontally extended terminal cell with equal arms (*A. distylum*). The external glands are either sessile or distinctly stalked, and sometimes the stalk merges into the head [1].

The investigation of the **petiole** by C. de Candolle and others shows that its system of vascular bundles forms a ring, and that within the latter further vascular bundles occur in certain species (*A. Pseudoplatanus, A. macrophyllum,* Pursh., *A. Negundo, A. mexicanum,* 'DC.').

3. STRUCTURE OF THE AXIS. In addition to the above-mentioned species of *Acer* I was able to examine *Dipteronia sinensis*, Oliv. (China, Henry), which, as will be mentioned immediately, agrees in the structure of its axis with the species of *Acer* in all essential points.

The medullary rays of the **wood** are narrow, at the most 4-seriate (in *A. Pseudoplatanus*), their cells being usually elongated in the radial direction. The vessels do not possess a large lumen (diameter = ·036 mm. in *A. platanoides*, ·06 mm. in *A. Pseudoplatanus*), and are always provided with simple perforations in their end-walls. The vessel-wall, where it is in contact with ray-parenchyma, is provided with bordered pits. Spiral thickening of the walls of the vessels has been observed in *A. platanoides, A. campestre, A. Pseudoplatanus, A. distylum,* and *A. Negundo.* The wood-parenchyma is developed to a limited extent. Chambered parenchyma containing crystals occurs in *A. campestre* and *A. platanoides.* The wood-prosenchyma has simple pits, and in *Acer* it sometimes contains starch. The filling of the lumina of the vessels with carbonate of lime in the heart-wood of *A. rubrum* and *A. illyricum* deserves notice; calcium carbonate is also met with in the cells of the pith in stems of *Acer* (Molisch).

The formation of cork is mostly superficial. In the cases investigated by me as well as by J. E. Weiss and others the cork originates in the outermost layer of cells of the primary **cortex** or in the layer immediately below; in those species of *Acer*, however, which excrete [2] wax on the surface of their branches, the cork originates in a somewhat deeper layer, namely from three to six layers below the epidermis, and only at a relatively late stage (Pax). The cells of the cork usually (*Acer, Dipteronia*) have rather wide lumina; in *Acer Negundo* cork-cells occur, which are sclerosed either on one or on all sides.

The primary cortex contains solitary crystals in *A. campestre* and *A. platanoides*, large clustered crystals in *A. distylum*, isolated stone-cells in *A. Negundo.* The varied structure of the pericycle is very noteworthy. In *A. Negundo* a composite and continuous ring of sclerenchyma is found in this region, in *A. Pseudoplatanus* a somewhat interrupted composite ring; in the other species investigated (*A. platanoides, A. campestre, A. spicatum, A. distylum*) as well as in *Dipteronia* only isolated groups of bast-fibres occur. The secondary bast in *A. campestre, A. Pseudoplatanus,* and others, as well as in *Dipteronia,* contains bundles of hard bast, which occasionally give rise to stratification of the phloem; groups of stone-cells and chambered parenchyma with solitary crystals also occur in the secondary bast of the species of *Acer.*

The outermost portion of the soft bast in certain species of *Acer* (*A. platanoides, A. campestre, A. distylum*) and also in *Dipteronia* contains the

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[1] Concerning the glandular nature of the leaf-teeth and leaf-tips of *A. Negundo* and *A. platanoides* respectively, see Reinke, loc. cit.

[2] The above-mentioned deposit of wax on the branches and stems in certain species of *Acer* (*A. Lobelii, A. Negundo, A. pennsylvanicum*), according to Uloth, arises by transformation of the walls of the epidermis and of the subjacent layers of the primary cortex.

secretory elements long known to occur in *Acer* and usually (even by Pax in his monograph) incorrectly termed laticiferous vessels; they have already been briefly mentioned above under the leaf-structure. These secretory elements are essentially simple cells; they are easily recognized in transverse section by their wide lumina and by their contents, which are whitish or occasionally (*A. distylum*) brownish in colour in dried material; they occur singly or in groups. In macerated sections of *Acer platanoides* I was just as unsuccessful as De Bary in finding any open communication between two neighbouring sacs by means of perforated lateral protrusions as mentioned by Hanstein; protrusions of the lateral cell-walls are not uncommonly present, but are never perforated, and the same is also true of the ends of the sacs. The secretory sacs in question are of varied length in the different species. In *A. platanoides* and *A. campestre* they are of considerable length, in the last-named species, according to De Bary, usually 1 mm. in length. They are much shorter in *A. distylum* and in *Dipteronia*, in which several can be observed situated one above the other, in the same radial section. It is worthy of note that the secretory sacs in *Dipteronia* also occur in the internal portion of the bast.

Literature: Hanstein, Milchsaftgef., Berlin, 1864, p. 20.—Chalon, Tig. ligu. dicotylèd., i. Mém., Gand, 1867, p. 11.—Uloth, Wachsbild., Flora, 1867, pp. 385 and 421 et seq. and Taf. vii.—Möller, Denkschr. Wiener Akad., 1876, pp. 87 and 383.—Reinke, Pringsheim Jahrb., Bd. x, 1876, p. 159.—De Bary, Vergl. Anat., 1877, p. 157.—Schmalhausen, Milchsaftbeh., Mém. Acad. imp. de St-Pétersbourg, sér. 7, t. xxiv, n. 2, 1877, pp. 20–2.—C. de Candolle, Mém. Soc. phys. et nat. de Genève, t. xxvi, 2, 1879, pp. 437, 438, and 460.—Molisch, Kohlens. Kalk, Sitz.-Ber. Wiener Akad., Bd. lxxxiv, Abt. 1, 1881, p. 14.—Möller, Rindenanat., 1882, pp. 267–71.—Solereder, Holzstr., 1885, p. 103.—Pax, Monogr. d. Gatt. *Acer*, Engler, Bot. Jahrb., Bd. vii, 1886, pp. 257, 258.—Plitt, Blattst., Diss., Marburg, 1886, p. 38.—Petit, Pétiole, Act. Soc. Linn. de Bordeaux, t. xliii, 1889, p. 29 and pl. i.—Radlkofer, Glied. d. Sapindac., Sitz.-Ber. Münch. Akad., 1890.—J. E. Weiss, Denkschr. Regensb. bot. Gesellsch., 1890, separate copy, p. 65.—Strasburger, Bau u. Verricht., 1891, pp. 215–18.—Zimmermann, Pflanzenzelle, 2. Heft, 1891, p. 51.—Pax, in Natürl. Pflanzenfam., 3. Teil, Abt. 5, 1893, pp. 264, 265.—Kuhla, Phelloderm, Bot. Centralbl., 1897, iii, p. 197.

MELIANTHACEAE.

This Order, which consists of the three genera *Melianthus*, *Bersama*, and *Greyia*, is characterized anatomically by the absence of both internal and external glands, by the lack of a specially constituted stomatal apparatus and of a sclerenchyma-ring in the cortex, by the possession of styloids or of bundles of raphides replacing them, by internal formation of cork, by simple-pitted wood-prosenchyma and simple perforations in the vessels. Medullary vascular bundles (Fig. 54) are present in certain species of *Bersama* and *Melianthus*[1].

The **leaves** (*Melianthus comosus*, Vahl, *M. major*, L., *M. minor*, L., and *Bersama abyssinica*, Fres.) are bifacial in structure. Gelatinization of the epidermis has not been observed. The stomata occur only on the lower surface of the leaf, and are surrounded by several epidermal cells of the ordinary shape. The vascular bundles of the veins are accompanied by sclerenchyma in *Bersama abyssinica* only. In *Melianthus*, as well as in *Bersama*, the mesophyll contains styloids especially at the limit of the palisade and spongy parenchyma; these styloids lie parallel to the surface of the leaf, and hence cannot cause transparent dots. The hairy covering of the leaves of *Melianthus minor* and *M. comosus* is formed by stellate hairs with four or more rays; these rays are unicellular and are sunk side by side in the epidermis.

Regarding the structure of the **wood**, the following facts may be pointed out in addition to what has already been said. The medullary rays of the wood are 3–4-seriate. In *Melianthus* the vessels attain a diameter of ·04 mm., in

[1] The following statements are based for the most part on my own investigations.

Greyia ·05 mm., in *Bersama* ·08–·09 mm. They have bordered pits, even where they are in contact with parenchyma of the medullary rays. The walls of the vessels of *Melianthus comosus* are spirally thickened. The wood-parenchyma is only slightly developed.

The cork arises in the middle of the primary **cortex** or still further inwards near the outer limit of the bast. In *Melianthus* and *Greyia* the cork-cells have wide lumina and delicate walls; in *Bersama* some of them have their outer tangential walls sclerosed. The outer limit of the bast in *Melianthus* is formed by collenchymatous tissue, in *Bersama* by isolated groups of bast-fibres; some of these fibres have fairly wide lumina and are septate by means of delicate division-walls. In the same region in *Greyia* isolated groups of sclerenchymatous cells occur, which are elongated in the vertical direction, and are intermediate between parenchyma and prosenchyma in form. Hard bast is absent from the secondary bast.

In the axis, as in the leaf, of *Bersama* and *Melianthus* styloids are found, and are present in the pith, bast, and primary cortex. In *Greyia*, on the other hand, raphides and clustered crystals occur, the former in the pith and bast

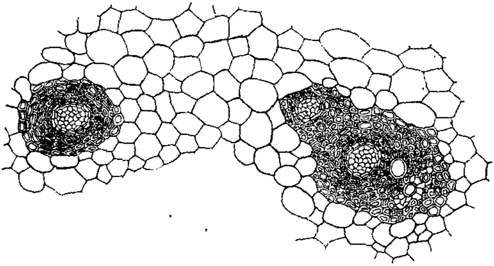

FIG. 54. Transverse section through a portion of the pith of *Melianthus major*, L. with medullary vascular bundles.—Original.

(bast-parenchyma), the latter in the pith, bast (in this tissue in chambered parenchyma), and in the primary cortex.

In conclusion, mention may be made of the occurrence of peculiar medullary vascular bundles in *Melianthus major* (but not in *M. minor* and *M. comosus*; see Fig. 54) as well as in *Bersama abyssinica* and *B. serrata*, Rich. These medullary bundles are concentric in structure. In a transverse section of the branch each of these bundles shows at its centre a group of soft bast, which is surrounded by a ring of wood-prosenchyma-cells, with simple pits, and occasionally septate. Only rarely is an isolated vessel found in the peripherally placed xylem-portion, which consists of wood-fibres. In the pith, bundles, consisting solely of a group of wood-prosenchyma, are sometimes also to be observed. As to the course of these medullary bundles, it is known from my earlier investigation of *Melianthus major* that they originate at the node by the entrance of portions of the normal bundle-ring into the pith. In *Bersama abyssinica* medullary bundles have also been observed in the petiole by C. de Candolle.

Literature: C. de Candolle, Mém. Soc. phys. et nat. de Genève, t. xxvi, 2, 1879, p. 460.—Solereder, Holzstr., 1885, pp. 103–5.—Radlkofer, Glied. d. Sapindac., Sitz.-Ber. Münch. Akad. 1890.—Gürke, in Natürl. Pflanzenfam., 3. Teil, Abt. 5, 1895, p. 375.—Gauchery, *Melianthus hybride*, Assoc. franç., Tunis, 1896, ii, pp. 421–8.

STAPHYLEACEAE.

This Order, which consists of the two tribes[1] Staphyleae (with the genera *Staphylea*, *Euscaphis*, *Turpinia*) and Akanieae (with *Akania*, *Huertea*, *Tapiscia*), is characterized anatomically by the absence of external as well as internal glands, by the lack of a composite and continuous ring of sclerenchyma in the pericycle (in place of which only isolated groups of primary bast-fibres are present) and by the tendency to the formation of scalariform perforations in the vessels. To the external morphological features of the tribes one essential anatomical character may be added: in the Staphyleae the wood-prosenchyma is provided with typical bordered pits, in the Akanieae with simple pits.

With regard to the detailed structure of the **leaf**, the following statements are based on the investigation of *Staphylea pinnata*, L., *Euscaphis staphyleoides*, Sieb. et Zucc., *Turpinia nepalensis*, Wall., *Akania Hillii*, Hook., and *Tapiscia sinensis*, Oliv. The mesophyll is bifacial in structure. The stomata occur only on the lower side of the leaf. In *Staphylea*, *Euscaphis*, and *Turpinia* they are usually wedged in between three neighbouring cells, according to the Cruciferous type; in *Akania* they are surrounded by several epidermal cells of the ordinary shape. In *Akania* the stomata are united into groups in small depressions of the leaf-surface; the epidermal cells situated between the pairs of guard-cells and concerned in the formation of the surface of the depression, are produced into long, slender papillae, the tips of which are differentiated in a crown-like form. Moreover a subpapillose epidermis is found on the lower side of the leaf of *Tapiscia*. Gelatinization of the inner wall has been observed in the upper epidermis of the investigated species of *Turpinia* and *Tapiscia*; in *Turpinia nepalensis* the mucilaginous epidermal cells are of spherical form and penetrate into the mesophyll. In *Staphylea*, *Turpinia*, and *Akania* the veins contain abundant bast-fibres accompanying the vascular bundles, while in *Euscaphis* sclerenchyma is absent in the veins. In the leaves of *Staphylea*, *Euscaphis*, and *Turpinia* oxalate of lime is present in the form of clustered crystals; in *Akania* numerous solitary crystals of the ordinary form are found in the veins. In *Euscaphis staphyleoides* short simple unicellular hairs occur on the leaf. Glandular hairs are wanting. The glandular leaf-teeth of *Staphylea pinnata* contain colourless mucilage-containing parenchyma, which surrounds the termination of a vascular bundle, and on the upper side of the leaf they bear a number of stomata in the otherwise unaltered epidermis (Reinke).

The **petiole** has been investigated by Petit in *Staphylea pinnata* and *S. trifolia*. Its characteristic region ('caractéristique') is distinguished by the fact that it contains a circular bundle-system, consisting of a large lower arc of wood and bast and of three upper smaller vascular bundles.

The structure of the axis has been investigated in the species of *Staphylea*, *Euscaphis*, *Turpinia*, *Akania*, *Tapiscia*, already named, and in *Huertea cubensis*, Griseb. The medullary rays of the **wood** are as a rule 4 cells in breadth, but are much broader in *Akania*. The vessels have a medium diameter, which in the different genera varies between ·045 mm. (*Huertea*) and ·075 mm. (*Akania*). In all the members of the Order with the exception of *Akania* the perforations of the vessels are exclusively scalariform and have numerous bars. In *Akania* the perforations of the vessels are usually simple and of elliptic or circular outline; besides these, however, scalariform perforations also occur and have numerous transverse bars, the latter being delicate and some of them anastomosing obliquely with one another. On the vessel-walls, which are in contact with ray-parenchyma, bordered pits occur alone, or in addition to unbor-

[1] With regard to the classification of the Staphyleaceae see Solereder, Ber. deutsch. bot. Gesellsch., 1892, loc. cit.

dered pits, the latter being of the same size as the borders of the former. In *Staphylea pinnata* the walls of the pitted vessels are provided with a loosely-wound spiral band. The wood-parenchyma is not prominently developed; in *Huertea* it is sometimes differentiated as chambered parenchyma with solitary crystals. The simple-pitted wood-prosenchyma of the genera belonging to the tribe Akanieae is sometimes septate by means of a few delicate division-walls.

Respecting the structure of the **cortex**, we may add to what has already been said in the introductory remarks, that the cork originates superficially, either in the epidermis itself (*Staphylea, Euscaphis*) or immediately below the epidermis (*Turpinia*). In *Akania Hillii* the whole of the bast is rich in sclerosed elements with the structure of bast-fibres. Groups of bast-fibres or isolated bast-fibres occur in the secondary bast of *Euscaphis, Huertea* and *Turpinia*, groups of stone-cells in the same tissue in *Turpinia* and, according to Möller, also in *Staphylea pinnata*. The sieve-plates are composed of sieve-areas, which are arranged in a scalariform manner. Solitary and clustered crystals have been observed in the cortex of *Akania* and *Huertea*, clustered crystals alone in the cortex of *Euscaphis, Staphylea*[1], and *Turpinia*. Lastly, mention may be made of the fact that the **pith** of *Tapiscia* contains numerous cells with mucilaginous membranes, which ultimately cause septation of the pith owing to the formation of lacunae.

Literature: Reinke, Sekretionsorg., Pringsheim Jahrb., Bd. x, 1876, p. 142.—Möller, Denkschr. Wiener Akad., 1876, pp. 385, 386.—Möller, Rindenanat., 1882, pp. 283, 284.—Solereder, Holzstr., 1885, p. 103.—Petit, Pétiole, Act. Soc. Linn. de Bordeaux, t. xliii, 1889, p. 28 and pl. i.—Radlkofer, Glied. d. Sapindac., Sitz.-Ber. Münch. Acad., 1890.—Solereder, Staphyl.-Gatt. *Tapiscia*, Sitz.-Ber. deutsch. bot. Gesellsch., 1892, pp. 545 *et seq.*—Pax, in Natürl. Pflanzenf., 3. Teil, Abt. 5, 1893, p. 258.

SABIACEAE.

Of the four genera of the Order *Sabia* and *Meliosma* have alone been investigated anatomically.

The following points may be mentioned with regard to the structure of the **leaf**[2]. In both genera the stomata are surrounded by several ordinary epidermal cells and are present only on the lower side of the leaf. The mesophyll has bifacial structure throughout. According to Dihm the palisade-tissue in all the investigated species of *Meliosma* is differentiated in the form of arm-palisade-parenchyma. The formation of folds in this case involves the upper part of the cells, and, when extensively developed, causes an appearance in the cells resembling a coral-stem. The vascular bundles of the veins are usually surrounded by a ring of sclerenchyma. Oxalate of lime is excreted in the form of clustered crystals only. Internal secretory organs are absent. The resin-cells, stated by Blenk to occur in the mesophyll of *Meliosma nitida*, Bl., and *M. simplicifolia*, Walp., are, according to a verbal communication of Radlkofer, cells with siliceous contents.

A **hairy covering** is rare in *Sabia*, more common in *Meliosma*. In *Sabia* (*S. campanulata*, Wall.) it consists of ordinary unicellular clothing hairs, in *Meliosma* of uniseriate trichomes, the lower cells of which are usually shorter than the upper, and of glandular hairs with a relatively long uniseriate stalk and an oblong unicellular head, which is occasionally divided by a vertical wall.

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[1] The statement as to the occurrence of crystal-sand in the cortex of *Staphylea*, quoted by Kohl (Kalksalze u. Kieselsäure etc., 1889, p. 34) from Sanio's work (Monatsber. Berliner Akad., 1857, p. 252), is incorrect.

[2] Numerous species of *Meliosma* have been investigated by Dr. Dihm, who will himself give a more detailed account of their structure; *Sabia leptandra*, Hook f. et Th., has been investigated by me. I owe the statements given in the text to verbal information from Dr. Dihm. See also Blenk, Flora, 1884, p. 369, pp. 81–83 of reprint.

The following account of the structure of the **axis** is based on recent investigations of my own, which are more comprehensive than the statements made in my 'Holzstruktur [1],' and extend to *Sabia campanulata*, Wall., *S. limoniacea*, Wall., *Meliosma simplicifolia*, Walp., and *M. Arnottiana*, Walp. Features common to both genera are: (*a*) the occurrence of scalariform perforations with fairly numerous bars (up to fifteen) in the vessels, side by side with which simple, often elliptically elongated, perforations are more or less frequent; and (*b*) the fairly large simple or bordered pits or the vessel-walls, where they are in contact with parenchyma. On the other hand, the two genera show essential differences in regard to other features in the structure of the axis. In *Sabia* the primary medullary rays are broad [2], so that the vascular bundles are distinctly separated from one another; the portions of the primary medullary rays situated between the groups of bast are sclerosed. In *Meliosma* the primary medullary rays are not specially broad, but are broadened outwards in the form of wedges between the groups of bast. In *Sabia* the wood-prosenchyma has thick walls with typical bordered pits; in *Meliosma* it has fairly wide lumina, provided in places with a few delicate division-walls, and bears simple pits. Lastly, in *Sabia* only, a composite and continuous ring of sclerenchyma is found at the outer limit of the bast; this ring consists of groups of elongated sclerenchyma-cells, which are of the nature of rod-cells, and of stone-cells. In the same region of the stem of *Meliosma* isolated primary groups of hard bast are alone present; in the radial direction these latter are connected with cells resembling bast-fibres and situated at the margins of the groups of bast, which they bound towards the medullary rays. Finally the primary cortex of *Meliosma* contains numerous stone-cells, which have lumina of varied size and are usually elongated in the direction of the axis; the origin of the cork is superficial in *Meliosma simplicifolia*.

ANACARDIACEAE.

1. Review of the Anatomical Features. The occurrence of resin-canals, which are situated in the bast of the vascular bundles of stem, root, and leaf, is characteristic of all true Anacardiaceae. The only exceptions are the genera *Corynocarpus* and *Juliania*, of which the latter is also anomalous in other respects: *Juliania* possesses only medullary balsam-canals in its branches, and should therefore probably be included in Simarubaceae. In addition to those in the bast, resin-canals are met with in the pith of certain species belonging to a large number of genera (see the section on the structure of the axis) and in the primary cortex of species of some few genera (*Anacardium, Dobinea, Holigarna*, and *Thyrsodium*). Tannin-sacs in the soft bast are of widespread occurrence throughout the Order; lysigenous mucilage-cavities are present in the primary cortex in species of *Campnosperma* (perhaps also in species of *Faguetia* and *Trichoscypha*: see under structure of axis). The wood is characterized by the predominant occurrence of simple perforations in the vessels, side by side with which scalariform perforations only occur in a few species; by the simple pits, often of large size, on the vessel-wall, where it is in contact with parenchyma; and by the simple-pitted and frequently septate wood-prosenchyma. The origin of the cork is in all cases superficial. In the pericycle isolated groups of bast-fibres are usually found; they are often arc-shaped, and in that case enclose the outermost resin-canals of the bast on their concave side; more rarely a composite and continuous ring of

[1] Holzstr., 1885, pp. 105–6; see also Warburg, in Natürl. Pflanzenfam., 3. Teil, Abt. 5, 1895, p. 367.
[2] Broad medullary may be seen with the naked eye in *S. lanceolata*, Colebr., *S. leptandra*, Hook. f. et Th. and *S. parviflora*, Wall.

sclerenchyma is found in place of the groups of bast-fibres. The stomata, so far as is known, possess no special subsidiary cells. Oxalate of lime is excreted in the form of ordinary solitary and clustered crystals. The hairy covering is formed by ordinary unicellular trichomes and by glandular hairs of most varied shape.

2. STRUCTURE OF THE LEAF. The **leaf-structure** has not yet been subjected to a thorough investigation, since the Order as such is already sufficiently characterized by certain anatomical features of the axis. Such an investigation will, however, give valuable data for the diagnosis of the species and genera, judging by the little that is at present known regarding the leaf-structure.

In *Mangifera indica*, L., as well as in *Spondias lutea*, L., the stomata are not accompanied by any special subsidiary cells. Among the many species of *Rhus* investigated, *R. acuminata*, DC., and *R. semialata*, Murray, alone, according to Radlkofer, possess papillae on the lower side of the leaf. The presence of small external glands on the surface of the leaf is described by Radlkofer in this Order (*Dobinea*, species of *Rhus*, *Buchanania*, *Phlebochiton*, &c.). In *Dobinea* they are small glands with a short stalk and an oval head of not very many cells. In the species of *Rhus* the glands are very variously shaped, and might furnish useful characters for specific distinction; for instance, I have met with the following forms in *Rhus*: peltate glands (similar to the well-known glands of the Oleaceae), which in certain species (e.g. *R. mucronata*, Thunb., or *R. lucida*, L.), according to Volkens, cover the leaves with a thin coating of varnish; secondly, external glands, which are rosette-like or almost resemble stellate hairs; further, club-shaped glands, which are uni- or bicellular; and finally, glands with a short uniseriate stalk and a spherical head of rather numerous cells. According to Engler, simple unicellular hairs are not uncommon. The vascular bundles of the veins are accompanied by solitary crystals in *Mangifera indica*, by clustered crystals in *Spondias lutea*. In the leaf-tissue of *Rhus succedanea*, L., *Spondias dulcis*, Forst., and of the genus *Tapirira*, Blenk mentions the occurrence of clustered crystals which cause distinct transparent dots. Transparent dots, due to secretory cavities, are entirely wanting in this Order. The secretory canals, which will be more fully discussed in the description of the axis, also accompany the vascular bundles in the leaf, where they are always found in the phloem, both of the larger and smaller veins; occasionally also, corresponding to the medullary resin-canals of the branches, they are found on the upper side of the wood, without ever passing from the veins into the mesophyll. In *Rhus semialata* and *R. glauca* Trécul observed that the secretory canals of the leaf anastomosed reticulately like the accompanying vascular bundles.

3. STRUCTURE OF THE AXIS[1]. With regard to the structure of the **wood**

[1] Most important literature: Engler, Solereder and Jadin, ll. cc. The above description is further based on more recent investigations of my own, which were made on the following material: *Buchanania sessilifolia*, Bl., *Mangifera indica*, L., *Anacardium occidentale*, L., *A. nanum*, St. Hil., *A. pumilum*, St. Hil., *Gluta elegans*, Hook. fil., *Swintonia glauca*, Engl., *Melanorrhoea usitata*, Wall., *Dobinea vulgaris*, Hamilt., *Bouea macrophylla*, Griff., *Spondias lutea*, L., *Dracontomelum sylvestre*, Bl., *Pleiogynium Solandri*, Engl., *Sclerocarya birrea*, Hochst., *Phlebochiton extensum*, Wall., *Odina Wodier*, Roxb., *Tapirira guianensis*, Aubl., *Haplorhus peruviana*, Engl., *Pistacia Lentiscus*, L., *Microstemon velutina*, Engl., *Pentaspadon Motleyi*, Hook. fil., *Thyrsodium Spruceanum*, Benth., *Faguetia falcata*, L. March., *Sorindeia madagascariensis*, P. Th., *Protorhus longifolia*, Engl., *Campnosperma gummifera*, L. March., *C. macrophylla*, Hook. fil., *Euroschinus falcatus*, Hook. fil., *Rhodosphaera rodanthema*, Engl., *Schinus molle*, L., *S. dependens*, Ortega, *Lithraea molleoides*, Engl., *Cotinus Coggyria*, Scop., *Loxostylis alata*, Spreng. fil., *Botryceras laurinum*, Willd., *Micronychia madagascariensis*, Oliv. (Herb. Kew), *Anaphrenium argenteum*, E. Mey., *Blepharocarya involucrigera*, F. Müll., *Comocladia ilicifolia*, Sw., *Metopium Linnaei*, Engl., *Pseudosmodingium perniciosum*, Engl., *Rhus Toxicodendron*, L., *R. retusa*, Zoll., *R. lancea*, L. fil., *R. typhina*, L., *Astronium fraxinifolium*, Schott, *Loxopterygium Sagotii*, Hook. f., *Schi-*

the following facts may be pointed out. The medullary rays are uni- or bi-seriate, at the most quadri-seriate, and are never very broad. The vessels possess lumina of varied size (maximum diameter = ·06 mm. in *Rhus Toxicodendron* to ·105 mm. in *Anacardium occidentale*). The perforations of the vessels are, as a rule, exclusively simple, and circular or elliptical. It is only in *Campnosperma*, *Micronychia*, and in *Anaphrenium argenteum* that scalariform perforations occur side by side with simple openings; in *Campnosperma* and *Micronychia* the former possess numerous bars and relatively wide perforated spaces between the bars, in *Anaphrenium* a very large number of delicate bars, and slit-like perforations. The walls of the vessels are provided with relatively large bordered pits (border having a diameter exceeding ·003 mm.) at those points where one vessel abuts on another; the border is smaller in the above-mentioned species of *Buchanania* and *Loxostylis* investigated by me, as also in *Sorindeia* and *Schinopsis*. The structure of the vessel-wall, where it is in contact with ray- or wood-parenchyma, is extremely characteristic. In these places simple pits, usually of large size, are chiefly found on the vessel-wall, and side by side with them transitional forms to true bordered pits, but never bordered pits alone. In many cases these simple pits are elliptical and placed transversely to the longitudinal axis of the vessel, lying parallel to one another, so that taken together they call to mind the scalariform perforation of a vessel (*Dobinea*, *Campnosperma*, *Loxostylis*). Spiral thickening of the vessel-wall has been observed in *Pistacia* (*P. Terebinthus*, L., and *P. Lentiscus*, L.). The prosenchyma forming the groundwork of the wood has simple pits. In the majority of the species investigated, the lumina of the cells of the wood-prosenchyma are wide, e.g. in *Sorindeia*, *Dracontomelum*, *Tapirira*; on the other hand, the cells of the wood-prosenchyma of *Lithraea*, *Melanorrhoea*, *Nothopegia*, *Astronium* and others possess narrower lumina. In many species the lumen of the wood-prosenchyma is locally septate; as examples I may mention among the species which I have examined those belonging to *Buchanania*, *Spondias*, *Dracontomelum*, *Pleiogynium*, *Phlebochiton*, *Tapirira*, *Microstemon*, *Thyrsodium*, *Protorhus*, *Schinus*, *Loxostylis*, *Rhus* (*R. lancea*), *Schinopsis*, *Loxopterygium*, *Dobinea*.

The origin of the **cork** is subepidermal in nearly all cases (namely in forty-five genera investigated by Jadin); in *Spondias*, *Protorhus*, and *Campnosperma* alone the cork arises somewhat deeper in the primary cortex, but still in a superficial layer of cells. Concerning the structure of the cork, Möller[1] mentions the following points. The cork-membranes are occasionally sclerotic either on one side (*Mangifera*, *Rhus*) or uniformly on all sides (*Schinus*) throughout several layers; *Pistacia* and *Odina* develop spongy cork consisting of cells with thin walls and wide lumina; *Astronium* has a periderm consisting of tabular cells with thick walls; in *Anacardium* scattered groups of cells become sclerosed in the cork, which is otherwise of a spongy nature, and composed of delicate cells. According to Möller, *Pistacia* and *Astronium* are characterized by extensive phelloderm-formation, the latter genus specially by the possession

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nopsis brasiliensis, Engl., *Nothopegia Colebrookiana*, Bl., *Drimycarpus racemosus*, Hook. f., *Semecarpus Anacardium*, L., *Holigarna Arnottiana*, Hook. f., *H. Helferi*, Hook. f., *H. ferruginea*, March. It may be added that Jadin in his most recent publication on the Anacardiaceae, apart from numerous species representing all the genera examined by me and cited above, for which reference must be made to the original, has likewise investigated genera which were not accessible to me, viz. *Solenocarpus*, *Pseudospondias*, *Poupartia*, *Cyrtocarpa*, *Haematostaphys*, *Trichoscypha*, *Mauria*, *Smodingium*, *Melanochyla*, *Corynocarpus* and *Juliania*, especially with regard to the structure of the cortex and the distribution of the balsam-canals.

[1] The statements from Möller's 'Rindenanatomie,' taken into account in what follows, refer to: *Pistacia Lentiscus*, L., *P. Terebinthus*, L., *Odina Wodier*, Roxb., *Schinus molle*, L., *Rhus Cotinus*, L., *R. typhina*, L., *R. Toxicodendron*, L., *Astronium* sp., *Mangifera indica*, L., *Anacardium occidentale*, L., *Spondias Birrea*, Rich.

of a phelloderm with regularly alternating layers of stone-cells and thin-walled cells.

The primary **cortex**, according to Jadin and my own investigations, contains sclerosed parenchyma in many cases. The latter tissue sometimes has thick walls, sometimes exceptionally wide lumina (as in the species of *Sorindeia, Campnosperma, Pleiogynium,* and *Melanorrhoea* investigated by me). In many species the stone-cells of the primary cortex unite to form a ring (species belonging to the genera *Spondias, Mangifera, Swintonia, Sclerocarya, Pseudospondias, Haematostaphys, Thyrsodium, Sorindeia, Campnosperma, Loxostylis, Smodingium, Astronium, Drimycarpus, Semecarpus,* and *Holigarna*).

The structure of the pericycle is characteristic. In the majority of the species it contains isolated groups of bast-fibres, usually in the form of an arc, the convex side being directed towards the exterior; on their inner side they include a single, and usually large, resin-canal. The primary arcs of bast-fibres in *Swintonia glauca,* Engl., and *Pseudospondias microcarpa,* Engl., communicate with each other in places by means of sclerosed parenchyma. In this way a transition is formed to the composite and continuous ring of sclerenchyma, which has only been met with in a few genera (*Gluta* pro parte, viz. in *G. elegans,* Hook. f., *Dracontomelum, Phlebochiton, Pistacia, Pentaspadon, Microstemon, Campnosperma, Euroschinus, Mauria, Lithraea, Metopium, Schinopsis,* and *Drimycarpus*) by Jadin and myself. In branches from the floral region this ring mostly includes the arcs of bast-fibres, which elsewhere appear isolated, and, in correspondence with this, it usually shows an undulated course in transverse section; exceptions to this are afforded by the species of *Pistacia* and *Lithraea* investigated by me.

With regard to the secondary bast Möller mentions three types. The secondary bast either lacks both bast-fibres and stone-cells (*Rhus*), or contains stone-cells but no bast-fibres (*Pistacia, Astronia*) or possesses bast-fibres with (*Mangifera, Odina, Anacardium*) or without (*Schinus*) stone-cells. In the secondary bast of the species investigated by me I have also frequently found a few scattered bast-fibres or bands of bast-fibres, or occasionally groups of hard bast united into a ring by groups of stone-cells.

Oxalate of lime occurs in the cortex in the form of clustered and solitary crystals. Chambered fibres containing solitary crystals occasionally (*Odina, Mangifera, Schinus*) occur in the bast, but chambered fibres with clustered crystals are wanting.

Amongst the **secretory organs** of the axis, the balsam-canals, which, according to Sieck, are schizolysigenous, may first be discussed. With the exception of the genera *Juliania* [1] and *Corynocarpus* [2] they are present in the bast of all the genera mentioned above. A large resin-canal occurs in the outermost portion of the bast of each vascular bundle; in a transverse section of the branch this canal is surrounded by the arcs of hard bast, mentioned above, their shape being that of a horse-shoe or almost annular, the latter e.g. in *Mangifera indica, Protorhus longifolia,* and *Botryceras laurinum.* Further, secretory canals also occur in the later-formed portions of the bast; these possess a smaller lumen and are arranged in concentric circles. According to Trécul (in *Schinus molle* and species of *Rhus*) and Jadin (in *Spondias dulcis*), they anastomose tangentially to form a network. In *Rhus viminalis,* according to Trécul, branches of the resin-canals, situated in the bast, penetrate into the medullary rays of the wood where they end blindly.

[1] According to Jadin (loc. cit., p. 96) *Juliania* only contains secretory canals in the pith and consequently probably belongs to the Simarubaceae.

[2] The monotypic genus *Corynocarpus,* included in the Anacardiaceae by Bentham and Hooker, possesses no secretory canals according to Jadin, and, if this is correct, must certainly be excluded from the Order.

In certain genera the resin-canals, besides occurring in the bast, are occasionally also found in the pith and still more rarely in the primary cortex. Concerning the occurrence of the medullary resin-canals Engler has already made numerous statements, and comes to the conclusion that they do not generally form a generic character, so that a natural division into genera with and without medullary resin-canals is impossible.

According to Engler, Jadin, and my own observations, the medullary resin-canals are present in: *Buchanania*, *Mangifera*, *Anacardium*, *Gluta*, *Swintonia*, *Spondias*, *Solenocarpus*, *Dracontomelum* (according to my own observations, and contrary to Jadin), *Pleiogynium*, *Sclerocarya*, *Pseudospondias*, *Poupartia*, *Phlebochiton*, *Odina*, *Cyrtocarpa*, *Haematostaphys*, *Tapirira*, *Harpephyllum*, *Pentaspadon*, *Microstemon*, *Thyrsodium*, *Faguetia*, *Sorindeia* pro parte, *Trichoscypha*, *Campnosperma*, *Euroschinus*, *Mauria* pro parte, *Schinus* pro parte, *Anaphrenium* pro parte, *Comocladia* pro parte, *Metopium*, *Pseudosmodingium*, *Rhus* pro parte, *Astronium*, *Loxopterygium*, *Schinopsis*, *Melanochyla*, *Drimycarpus*, *Semecarpus*, and *Holigarna* [1]. Their number often varies considerably even in the same genus (*Rhus*), and within certain limits even in different internodes of the same plant.

The resin-canals in the primary cortex have only been observed in a few species, namely, in *Dobinea vulgaris*, Ham., and *D. Delavayi*, Baill., in *Thyrsodium Schomburgkianum*, Benth. (but not in *T. Spruceanum*), further in *Holigarna Arnottiana*, *H. Helferi*, and *H. ferruginea*, as well as in numerous species of *Anacardium* (e.g. *A. occidentale*, L.). It is worthy of note that they are accompanied by cells of the nature of bast-fibres in the species of *Holigarna* mentioned, and in *Anacardium occidentale*.

Besides the resin-canals the tannin-sacs which, according to Engler and Jadin, occur more or less abundantly in the phloem of all members of the Order, must be mentioned. They are nearly always of considerable length, viz. 2–6 times as long as the surrounding parenchymatous cells. Finally, I have observed lysigenous mucilage-spaces in the primary cortex of *Campnosperma macrophylla*.

The resin-spaces, mentioned by Engler in *Campnosperma gummifera*, March., and *C. zeylanica*, Thw., and the 'glandes sécrétrices' described by Jadin in *C. seychellarum*, March., and *C. zeylanica*, Thw., are undoubtedly the same as the mucilage-spaces. On the other hand, it must for the present remain doubtful to which class of secretory organs the 'glandes sécrétrices corticales,' observed by Jadin in *Trichoscypha lucens*, Oliv., and *Faguetia falcata*, March., belong.

Note.—The **root** contains a single wide balsam-canal within each of the primary bast-portions, and, in the secondary bast, resin-canals with small lumina.

Literature: N. Müller, Vert. d. Harze etc., Pringsheim Jahrb., Bd. v, 1866–7, pp. 408–12.—Trécul, Vaiss. propres dans les Térébinth., Compt. rend., t. lxv, 1867, p. 27 et seq., Ann. sc. nat., sér. 5, t. vii, 1867, p. 112 et seq. and Adansonia, t. vii, pp. 121–31.—Van Tieghem, Canaux sécrét., Ann. sc. nat., sér. 5, t. xvi, 1872, pp. 168–72.—Möller, Denkschr. Wiener Akad., 1876, pp. 96–8 and 392.—De Bary, Vergl. Anat., 1877.—Engler, Gatt. *Rhus* etc., Engler, Bot. Jahrb., Bd. i, 1881, pp. 365–426.—Möller, Rindenanat., 1882, pp. 313–21.—Blenk, Flora, 1884, pp. 366 et seq., separate copy, pp. 79–81.—Solereder, Holzstr., 1885, pp. 106–7.—Leblois, Ann. sc. nat., sér. 7, t. vi, 1887, pp. 294 to 296.—Radlkofer, *Dobinea*, Sitz.-Ber. Münch. Akad., 1888, pp. 385–95.—Borowski, Anat. Bau etc. des Holzes von *Pistacia mutica*, Jahrb. d. Petersb. Forst-Instit., Bd. ii, 1888, pp. 1–39, Russian; abstract in Bot. Centralbl., 1889, ii, p. 794.—Douliot, Ann. sc. nat., sér. 7, t. x, 1889, p. 348.—Morot, *Podoon*, Journ. de Bot., 1889, p. 388.—Petit, Pétiole, Act. Soc. Linn. de Bordeaux, t. xliii, 1889, p. 28.—Radlkofer, Glied. d. Sapindac., Sitz.-Ber. Münch. Akad., 1890.—Volkens, Lack. Bl., Ber. deutsch. bot. Gesellsch., 1890, p. 130.—Engler, in Natürl. Pflanzenfam., iii. Teil, Abt. 5, pp. 139–41.—Jadin, *Dobinea* et *Podoon*, Journ. de Bot., 1893, pp. 250–6.—The same, Contrib. à l'étude des Térébinth., Montpellier, 1894, 97 et seq.—The same, Struct. et affin. des Térébinth., Ann. sc. nat., sér. 7, t. xix, 1894, p. 1 et seq.—Sieck, Pringsheim Jahrb., Bd. xxviii, 1895, p. 227 et seq.—Engler, Natürl. Pflanzenfam., Nachtr. u. Reg., Teil ii–iv, 1896, p. 216.—Kuhla, Phelloderm, Bot. Centralbl., 1897, iii, p. 196.—[Diels, Epharmose d. Veg.-Org. bei *Rhus* L., § Gerontogeae, Engl., Engler, Bot. Jahrb., Bd. xxiv, 1898, pp. 568 et seq. and Tab. xiv.]

[1] Jadin's statement concerning the occurrence of medullary resin-canals in *Melanorrhoea Beccarii*, Engl., and *M. usitata*, Wall., is incorrect according to my investigations on accurately determined specimens of these species.

CORIARIEAE.

This Order, consisting of only one genus (*Coriaria*) with few species, possesses the following anatomical features, which have been investigated in detail especially in *Coriaria myrtifolia*, L.

The stomata, which in *C. myrtifolia* occur on both surfaces of the **leaf**, are adjoined on either side by a single subsidiary cell, parallel to the pore. The outlines of the cells of both upper and lower epidermis are polygonal in the species named; the leaf-tissue is nearly centric and almost entirely formed of palisade-tissue. Oxalate of lime appears to be absent from the leaf; in the axis, on the other hand, it has been observed (in the medullary rays of the bast) in the form of solitary crystals. The leaf is rich in tannin and is consequently made use of technically (as sumach). Trichomes are wanting in *Coriaria myrtifolia*, but are present in *C. nepalensis*, Wall., and *C. thymifolia*, Humb. et Bonpl., in the form of papillae of bladder- or finger-like shape. Glandular hairs do not occur.

A transverse section of the **wood** shows broad medullary rays, which are as much as seven cells in breadth, and vessels with a diameter of as much as ·105 mm. The cells of the medullary rays are elongated in the vertical direction; the end-walls of the vessels have simple perforations. The wood-prosenchyma has simple pits.

With regard to the structure of the wood the species of *Coriaria* may, according to Russow, be divided into two groups. The first of these, which comprises the species of the Northern hemisphere (*C. myrtifolia*, L., *C. japonica*, A. Gray, *C. sinica*, Maxim, and *C. nepalensis*, Wall.), these being the species which develop their inflorescences on the branches of the previous year, is characterized by the fact that the primary medullary rays do not reach as far as the pith, but are separated from it by strongly thickened interfascicular tissue, which in transverse section appears like wood-prosenchyma. On the other hand, in the species of the second group, formed by those of the Southern hemisphere (*C. microphylla*, Poir., *C. ruscifolia*, L., and *C. sarmentosa*, Forst., the inflorescences of which develop on the branches of the current year), the parenchyma of the primary medullary rays penetrates as far as the pith.

In *Coriaria* the outer limit of the bast is formed by massive isolated groups of bast-fibres. The cork of *C. myrtifolia* arises immediately below the epidermis.

As to the affinities of the Order, which are still uncertain, the above anatomical features give no further information.

Literature: Russow, Anat. Bau der Laubspr. der C., Sitz.-Ber. Dorpater Naturf.-Gesellsch., Bd. vi, 1884, pp. 87–94.—Solereder, Holzstr., 1885, p. 107.—Engler, Natürl. Pflanzenfam., 3. Teil, Abt. 5, 1892, p. 129.

MORINGEAE.

The following points may be mentioned with regard to the anatomy of this small Order, which, like the last, consists of only one genus (*Moringa*).

The leaf (*M. pterygosperma*, Gaertn.) bears stomata without special subsidiary cells, and simple unicellular hairs with blunt tips. Glandular hairs are absent.

Noteworthy features in the structure of the wood (*M. aptera*, Gaertn., *M. pterygosperma*) are: that the vessels have simple perforations and simple pits, especially where they are in contact with parenchyma, and that the wood-prosenchyma is simple-pitted. In the pericycle of the two species named, there are groups of prosenchymatous cells, which have wide lumina and are strongly developed in the radial direction; in *M. pterygosperma* alone they are united by lignified parenchymatous cells with wide lumina into a broad strengthening ring.

Oxalate of lime is excreted in the leaf in the form of clustered crystals, in

the axis in the form of solitary and clustered crystals. Mucilage-canals are present in the pith in *M. pterygosperma* (one at the centre of the pith) and in *M. aptera* (two such); further, according to Pax, lysigenous mucilage-cavities occur in the cortex, and, according to Volkens, mucilaginous epidermal cells in the leaf (*M. aptera*).

Literature: Solereder, Holzstr., 1885, p. 107.—Volkens, Aegypt.-arab. Wüste, 1887, p. 115.—Pax, in Natürl. Pflanzenfam., 3. Teil, Abt. 2, 1891, p. 242.

CONNARACEAE.

1. Review of the Anatomical Features. According to the investigations hitherto published the anatomical features common to the members of this Order are: the simple perforations of the vessels, the simple pitting of the locally septate wood-prosenchyma, the simultaneous occurrence of simple and bordered pitting on the vessel-walls, where they are in contact with parenchyma, the superficial formation of periderm, the composite and continuous ring of sclerenchyma in the pericycle, the restriction of the stomata to the lower side of the leaf, and the manner of excretion of oxalate of lime, viz. in the form of solitary crystals (no clustered crystals). The stomata belong to different types as regards their neighbouring cells (see below). Internal secretory organs are represented by mucilaginous epidermal cells in the leaf (species of *Agelaea*, *Cnestis*, *Connarus*, *Bernardinia*, and *Rourea*), by lysigenous secretory cavities with resinous contents both in the leaf and in the floral organs (*Connarus*), by secretory cells in the leaf (*Agelaea*, *Byrsocarpus*), by tannin-sacs in the bast of the axis (*Connarus*), and by groups of cells with mucilaginous membranes (*Rourea*). The hairy covering (Fig. 55) is formed by two-armed or one-armed unicellular hairs (species of *Connarus*, *Rourea*, *Bernardinia*, *Byrsocarpus*), by branched hairs which in part show sympodial structure (species of *Connarus*), by trichomes resembling tufted hairs (*Agelaea*), and by ordinary unicellular hairs (*Rourea* pro parte and Cnestideae). Glandular hairs have hitherto been met with only in the floral organs (calyx of *Rourea Martiana*, Bak.).

The following special features of the leaf-structure require mention here: the varied form of the stomata and the varied nature of the adjoining cells (several ordinary neighbouring cells: *Connarus*, *Ellipanthus*; stomata together with their subsidiary cells, wedged in between three epidermal cells: *Rourea*, *Agelaea*, *Bernardinia*; stomata with subsidiary cells, parallel to the pore: *Cnestis*); the papillose nature of the lower epidermis (*Cnestis ramiflora*, Griff., and *Pseudoconnarus*); the sclerenchymatous hypoderm on the upper side of the leaf (*Connarus* pro parte); the conversion of the epidermis into two or three layers by means of secondary divisions (species of *Rourea*).

2. Structure of the Leaf. We owe our knowledge on this subject to Radlkofer's researches, which are followed here.

The **stomata** are restricted to the lower side of the leaf. The form of the guard-cells and the arrangement of the neighbouring cells with reference to them vary. In *Connarus* the stomata are provided with a front cavity, which is widely opened, and often at the same time very large; they are surrounded by about six epidermal cells, which are of equal size and are similar to the remaining cells of the epidermis (encircled stomata = 'umkränzte Spaltöffnungen'). In *Rourea*, on the contrary, especially in the American species of the genus, the stomata, which are completely covered in by two subsidiary cells, are provided with an elongated and narrow front cavity and occasionally with an external pore, connected with the former; in certain species (*Rourea frutescens*, Aubl., *R. glabra*, H. B. K., *R. oblongifolia*, Hook. et Arn., and *R. revoluta*, Planch.) the stoma together with its subsidiary cells is wedged in between three narrow cells; *Agelaea* and *Bernardinia* have their stomata similarly surrounded. Among

the Cnestideae, *Cnestis* possesses narrow stomata with subsidiary cells placed on either side and parallel to the pore, while *Ellipanthus tomentosus*, Kurz, has encircled stomata. The detailed structure of the **epidermis** presents a few other noteworthy anatomical features, namely: formation of papillae on the lower epidermis of the leaf (*Pseudoconnarus, Cnestis ramiflora*, Griff.); occurrence of mucilaginous epidermal cells (in *Connarus monocarpus*, L., and *Agelaea Wallichii*, Hook. f., in small numbers; regularly in *Rourea* and *Bernardinia*, but not in *Byrsocarpus*; among the Cnestideae in *Cnestis glabra*, Lam., and *C. ramiflora*, Griff., but not in *Ellipanthus tomentosus*); development of **hypoderm** of a special kind on the upper side of the leaf. In the species of *Connarus* to be mentioned later (see the table at the end of the leaf-structure), e.g. *C. favosus*, Planch., the hypoderm consists of a layer of short sclerenchyma-fibres, which is connected with the plates of sclerenchyma by means of which the bundles of the veins are vertically transcurrent. In numerous species of *Rourea* (*R. frutescens*, Aubl., *R. glabra*, H. B. K., *R. revoluta*, Planch., *R. oblongifolia*, Hook. et Arn., *R. camptoneura*, Radlk., and *R. pubescens*, Radlk.) the hypoderm shows a different structure; here the epidermis becomes 2–3-layered, especially on the upper side of the leaf, through the appearance of division-walls parallel to the leaf-surface; this duplication may either be local or may extend to all the epidermal cells with the exception of those which are most strongly and probably very early gelatinized.

Of internal **secretory elements** the following have been observed: firstly, rather large secretory cells (with contents resembling gum-resin) in *Agelaea Lamarcki*, Planch., and *A. Koneri*, O. Hoffm. et Hildebr., in which they may be observed as whitish dots after cutting the leaf; secondly, mucilage-cells (?) on the lower side of the leaf of *Byrsocarpus Pervilleanus*, Baill., in the neighbourhood of the vascular bundles, especially those of the median vein; thirdly, lysigenous secretory cavities in *Connarus* (excl. *C. fecundus*, Bak. = *Pseudoconnarus*, Radlk.). The secretory cavities contain a brown doubly refractive resin, which is readily soluble in ether and possesses a radiate structure; they are mostly situated in the middle of the mesophyll and usually only cause transparent dots after the leaf has been cut into from the lower side. In most of the species they are found both in the leaves and in the floral organs; but in other species they are restricted to the leaves (e.g. in *C. confertiflorus*, Bak.) or to the floral organs (e.g. in *C. erianthus*, Bak.).

In the leaf **oxalate of lime** is never present in the form of clustered, but only of ordinary solitary crystals. The latter occur in the leaf of certain species of *Cnestis* and *Agelaea* (*C. glabra, C. ramiflora, A. pentagyna, A. Koneri*) in unusual numbers and are of conspicuous size. The mucilaginous membrane of the epidermal cells of *Rourea amazonica*, Radlk., and *R. patentinervis*, Radlk., is covered with numerous small crystals of oxalate of lime (a kind of crystal-sand).

The form of the **clothing hairs** (Fig. 55) is rather varied. In most species of *Connarus* the unicellular trichomes are distinctly, although often unequally, two-armed, and occur both on the leaf and on the inflorescences and floral organs (Fig. 55, *A–B*); occasionally, however, by reduction on one side they may become one-armed (Fig. 55, *C*). In other species of *Connarus* the hairs are articulated and branched (Fig. 55, *D–F*), their component cells being either elongated and protruded laterally at special points to form long branches, or short and each drawn out in its entirety to produce a branch, the axial part of the hair being built up in the manner of a sympodium by the basal parts of the joint-cells. *Rourea* (*R. frutescens*, Aubl. and its allies) and *Bernardinia* possess very unequally two-armed, or one-armed unicellular hairs; in *Rourea* (*R. induta*, Planch., &c.), however, ordinary unicellular hairs also occur. In *Agelaea*, curly trichomes are in some cases (*A. pentagyna, A. Koneri*) present; these are united at their base in pairs or several together, and appear

to be derived from two-armed hairs, whilst they constitute a transition to tufted hairs; in other cases (fruit of *A. Wallichii*) one-armed hairs like those of *Connarus* occur. In *Byrsocarpus* the trichomes on the lower side of the leaf form transitions from one-armed to very unequally two-armed hairs. *Cnestis*, as also *Ellipanthus* and perhaps all the Cnestideae, have simple, bristle-like, unicellular hairs, in which the lumen is enlarged at the base.

The following is a review of the anatomical features of the leaf in the American species of *Connarus*, according to Radlkofer:

A. Hairs two-armed or almost two-armed: (*a*) Sclerenchymatous hypoderm: *C. favosus*, Planch.; (*b*) Without hypoderm: *C. guianensis*, Lamb., *C. Schomburgkii*, Planch., *C. Sprucei*, Bak., *C. ruber*, Bak., *C. panamensis*, Griseb., *C. Blanchetii*, Planch., *C. marginatus*, Planch., *C. Beyrichii*, Planch., *C. cuneifolius*, Bak., *C. nodosus*, Bak., *C. Patrisii*, Planch., *C. cymosus*, Planch.

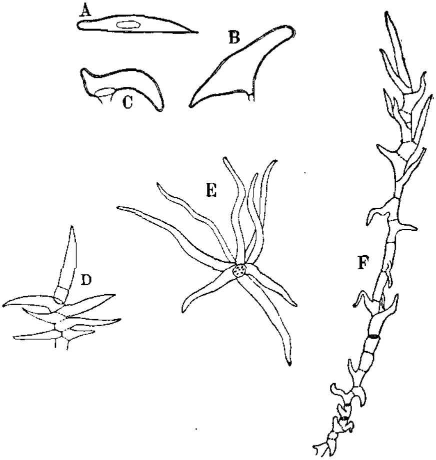

FIG. 55. A–C, Two-armed and one-armed trichomes of *Connarus Blanchetii*, Planch. D–F, Branched hairs of species of *Connarus*: D–E, *Connarus fulvus*, Planch., F, *Connarus pachyneurus*, Radlk.; the trichome in E, is seen from above, that in D and F from the side.—Original.

B. Branched hairs: (*a*) Without secretory cavities; hairs not distinctly sympodial: *C. pachyneurus*, Radlk., *C. erianthus*, Bak.; (*b*) with secretory cavities; hairs often distinctly sympodial; (*aa*) Sclerenchymatous hypoderm: *C. suberosus*, Planch., *C. fulvus*, Planch.; (*bb*) Without hypoderm: *C. confertiflorus*, Bak., *C. Perrottetii*, Planch., *C. detersus*, Planch.

3. STRUCTURE OF THE AXIS. The following points may be mentioned with regard to the structure of the wood, which I have examined in species of *Cnestis*, *Cnestidium*, *Ellipanthus*, *Rourea*, and *Connarus*. In *Cnestidium lasiocarpum*, Bak., the medullary rays are 1–5 cells broad; in all other cases they are only uni- or biseriate. The diameter of the vessels, which have rounded lumina, and are mostly isolated, varies (maximum diameter = ·045 mm. in *Ellipanthus Helferi*, Hook. fil., ·08 mm. in *Cnestis glabra*, Lam., &c.). The perforations of the vessels

are always simple; the vessel-wall, where it is in contact with parenchyma, is provided with simple or bordered pits. The wood-prosenchyma is simple-pitted and is occasionally septate in all the species. The wood-parenchyma is little developed or is absent. This tissue (*Cnestidium*), like the wood-prosenchyma (*Cnestis, Cnestidium*), occasionally contains solitary crystals.

The structure of the **cortex** was investigated by me in *Connarus fulvus* and *Rourea induta*. In both species the cork arises subepidermally and is composed of cells with fairly wide lumina. The pericycle in both species contains a composite and continuous ring of sclerenchyma; the secondary bast in *Connarus fulvus* includes tangential groups of tannin-sacs with wide lumina, similar to those of many Leguminosae; in *Rourea induta* it contains secondary groups of hard bast. The primary cortex of *Rourea induta* is characterized by the presence of mucilage-spaces, which are apparently formed by cells with mucilaginous membranes. Clustered crystals are wanting in the axis, as in the leaf.

Literature: Solereder, Holzstr., 1885, p. 108.—Radlkofer, Durchsichtige Punkte u. andere anat. Charakt. der C., Sitz.-Ber. Münch. Akad., 1886, pp. 343-78 and Durchs. P., loc. cit., p. 316.—Gilg, in Natürl. Pflanzenfam., 3. Teil, Abt. 3, 1890, p. 62.—H. Schenck, Anat. d. Lianen, 1893, p. 158.

LEGUMINOSAE.

The anatomy of the three sub-orders of the Leguminosae, the Papilionaceae, Caesalpinieae, and Mimoseae, will be discussed separately in what follows. Here it need only be pointed out that certain features in the structure of the wood are common to all the Leguminosae, namely simple perforations in the vessels and simple-pitted wood-prosenchyma. Reference may also be made to certain anatomical features, which will in some cases facilitate the determination of a sterile Leguminous plant as a member of the Papilionaceae or Caesalpinieae or Mimoseae. The tannin-sacs (Fig. 56), which have wide lumina filled with brown albuminous contents and are very widely distributed in the Papilionaceae, or corresponding elements with different contents, are met with in the Mimoseae, but are not found, or only show rudimentary differentiation, in the Caesalpinieae. The ordinary hairy covering of the Papilionaceae consists of simple uniseriate hairs, which possess one or several short basal cells and a long terminal cell (Fig. 59, *A–D*). Trichomes of this kind have not been observed in the Caesalpinieae or Mimoseae; in place of them in these sub-orders ordinary unicellular hairs, which appear to be absent in the Papilionaceae, very frequently occur. A third anatomical feature, which is of value for this purpose, is the manner of excretion of oxalate of lime: in the Papilionaceae it is found almost solely in the form of ordinary or of small rod-like solitary crystals, while in the Caesalpinieae, besides solitary crystals, clustered crystals frequently also occur; in the Mimoseae, clustered crystals have only been observed in the genera *Mimosa* and *Piptadenia*, elsewhere only solitary crystals.

I. PAPILIONACEAE.

1. Review of the Anatomical Features. Anatomical characters, which, according to the investigations hitherto made, are characteristic of all the Papilionaceae with but few exceptions, are not numerous. Such are: the simple perforations of the xylem-vessels, the simple pitting of the wood-prosenchyma, the absence of clustered crystals, and the lack of ordinary unicellular hairs[1]. Besides these anatomical features the following may be noted as indicating that a plant belongs to this suborder: the occurrence of styloid-like or

[1] If one disregards the papillae occasionally differentiated like hairs on the leaves of certain species.

small rod-like crystals and of elongated sac-like cells, which usually contain tannin and proteid and in the dried leaf are coloured brown ('tannin-sacs,' Fig. 56), two characters, however, which by no means belong to all the members of the Papilionaceae, but only to some of them.

In other respects very varied anatomical features are found. In some of the species the stomata are provided with subsidiary cells, which are directed parallel to the pore, in others the stomata are surrounded by ordinary epidermal cells without special orientation. The smaller veins of the leaf are in some cases embedded, in others vertically transcurrent. The place of origin of the cork is very varied; thus it may be the first cell-layer of the primary cortex or a deeper one, occasionally a middle zone or the innermost layer, while in some cases the development of cork even takes place in the pericycle on the inner side of the primary hard bast. At the outer limit of the bast either isolated groups of bast-fibres occur, or a ring of bast-fibres, or in many cases, a composite and continuous sclerenchyma-ring. The secondary bast is frequently stratified into hard and soft bast.

Internal secretory organs of varied nature are present. In many species the same contents that occur in the above-mentioned tannin-sacs occupy special idioblasts, which belong to the leaf-tissue, and are situated in the palisade tissue, or form a middle layer in the mesophyll, or the lowermost layer of the leaf-tissue. Secretory cells with other contents have been observed in the genera *Hallia, Lonchocarpus, Machaerium, Mundulea, Muellera, Pongamia, Sophora,* and *Tephrosia.* Secretory cavities occur in the genera *Amicia, Amorpha, Apoplanesia, Dalea, Derris, Dipteryx, Eysenhardtia, Lonchocarpus, Marina, Milletia, Muellera, Myrospermum, Myroxylon, Petalostemon, Piscidia, Poiretia, Pongamia, Psoralea, Pterodon,* and *Zornia*; in some species of *Derris, Lonchocarpus,* and *Piscidia* they are characterized by a papillosely differentiated epithelium (Fig. 57, *B*); in *Psoralea* the secretory cavities are intramural glands (Fig. 57, *A*), and in certain species of *Derris, Lonchocarpus, Milletia,* and *Pongamia* they are peculiar spherical secretory spaces (Fig. 57, *C*), which are surrounded by a loose envelope of cells curved like meridians on a globe. Resin-canals are rare (*Milletia auriculata,* Bak., *Myroxylon Pereirae,* Klotzsch); lysigenous gum-canals occur in the wood of *Herminiera.* In this connexion we may mention the formation of tragacanth in the species of *Astragalus,* the occurrence of an amyloid-like body in *Astragalus brachycalyx,* Fisch., and of indigo.

Oxalate of lime occurs chiefly in the form of ordinary solitary or small rod-like crystals (Fig. 58, *A*), while small crystalline granules or prisms, sphaerites (*Discolobium*), and clustered crystals appear very rarely. The crystals—especially when small and rod-shaped—are very frequently inserted in thickenings of the walls of the cells which contain them.

The hairy covering (Fig. 59) consists of clothing and glandular hairs. The usual form of the clothing hairs is that of simple uniseriate trichomes with one or several short basal cells and a long terminal cell (Fig. 59, *A–C*). Special forms of the clothing hairs are as follows: two-armed hairs (*Astragalus, Cyamopsis, Diplotropis, Erythrina, Gueldenstaedtia, Indigofera, Lessertia, Sphaerophysa, Swainsona*), the walls of which (excluding *Diplotropis* and *Erythrina*) are frequently encrusted with carbonate of lime; the branched trichomes of *Erythrina* (Fig. 59, *E*), consisting of basal cells and a branched terminal cell, and the branched unicellular hairs on the branches of species of *Dipteryx* (Fig. 59, *F*); hooked hairs (*Alysicarpus, Barbieria, Canavalia, Centrosema, Clitoria, Desmodium, Eleiotis, Leptodesmia, Lourea, Mecopus, Ougeinia Periandra, Phaseolus, Pictetia, Pseudarthria, Pycnospora,* and *Uraria*); the multiseriate shaggy hairs of *Aeschynomene, Arachis, Chapmannia, Discolobium, Geissaspis, Ormocarpum, Smithia,* and *Stylosanthes,* and the anchor-like shaggy hairs

of *Cranocarpus* (Fig. 59, *G*), which have an extremely characteristic structure. The glandular hairs also possess varied structure; at this point special mention need only be made of the peltate glands of species of *Centrolobium* and *Indigofera* (Fig. 59, *M*), which enclose an intercellular secretory space.

A whole series of special anatomical features are suitable for the more detailed diagnosis of Papilionaceae. Of these the following should be mentioned: the papillose differentiation of the epidermis of the leaf; the gelatinization of the epidermal cells of the leaf; the development of hypoderm in the leaf, which is, however, rare; the restriction of stomata to the upper side of the leaf, peculiar to *Geoffroya spinosa*, Jacq.; the transverse position of the stomata on the phylloclades and branches of *Carmichaelia australis*, R. Br., and of species of *Alhagi*; the occurrence of sclerenchyma-fibres (species of *Ammodendron, Andira, Bowdichia, Ormosia, Platymiscium Swartzia*), of spicular cells (species of *Swartzia*) and of mucilaginous cells (*Petalostemon*) in the mesophyll; the occurrence of crystals in the epidermis of the leaf in many species, and in a specially characteristic manner in *Canavalia* (Fig. 58, *C*) and *Stylosanthes* (Fig. 58, *B*); the various detailed features of the structure of wood and cortex; the tier-like construction of the wood in some species; the peculiar composition of the wood in some aquatic forms (species of *Aeschynomene, Erythrina, Geissaspis, Herminiera,* and *Soemmeringia*, cf. Fig. 60); the occurrence of cortical vascular bundles.

In connexion with the last-named anatomical feature, the anomalies of the stem-structure in some Papilionaceous lianes may also be mentioned. These consist in the appearance of successive rings of vascular bundles (*Dalbergia, Derris, Machaerium, Mucuna, Pachyrhizus, Pueraria, Rhynchosia, Spatholobus,* and *Wistaria*), in the formation of phloem-tissue in the wood (*Dioclea, Mucuna,* and *Phaseolus*), in the development, in centripetal order, of strands of wood and bast in the secondary cortex (*Dalbergia*, Schenck's stem, No. 495), and in the occurrence of a composite xylem-mass (piece of stem, Martius, No. 254, undetermined, see Fig. 62).

2. Structure of the Leaf. A thorough systematic investigation of the anatomy of the leaf has been undertaken in the more important tribes of the Papilionaceae, especially those which include the woody plants; thus the Phaseoleae [1] have been investigated by Debold, the Galegeae [2] by Weyland, the Hedysareae [3] by Vogelsberger, and the Dalbergieae, Sophoreae, and Swartzieae [4] by Köpff. The following description is based chiefly on these works, in addition to the scattered statements in the literature.

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[1] Material investigated: species of *Centrosema, Periandra, Clitoria, Cologania, Amphicarpaea, Dumasia, Shuteria, Glycine, Teramnus, Hardenbergia, Kennedya, Platycyamus, Erythrina, Rudolphia, Strongylodon, Apios, Mucuna, Butea, Spatholobus, Calopogonium, Cymbosema, Grona, Galactia, Camptosema, Cratylia, Dioclea, Cleobulia, Pueraria, Canavalia, Physostigma, Phaseolus, Vigna, Voandzeia, Pachyrhizus, Psophocarpus, Dolichos, Cajanus, Fagelia, Dunbaria, Atylosia, Cylista, Rhynchosia, Eriosema, Flemingia.*

[2] Species of *Psoralea, Eysenhardtia, Amorpha, Dalea, Petalostemon, Cyamopsis, Indigofera, Harpalyce, Brongniartia, Peteria, Barbieria, Galega, Tephrosia, Mundulea, Milletia, Wistaria, Robinia, Poitea, Olneya, Corynella, Diphysa, Sabinea, Coursetia, Cracca, Sesbania, Carmichaelia, Clianthus; Sutherlandia, Lessertia, Swainsona, Sphaerophysa, Colutea, Halimodendron, Caragana, Calophaca, Gueldenstaedtia, Astragalus, Oxytropis, Biserrula, Glycyrrhiza.*

[3] Species of *Scorpiurus, Hammatolobium, Ornithopus, Coronilla, Hippocrepis, Eversmannia, Hedysarum, Taverniera, Onobrychis, Ebenus, Alhagi, Chaetocalyx, Nissolia, Poiretia, Amicia, Pictetia, Ormocarpum, Herminiera, Aeschynomene, Soemmeringia, Smithia, Geissaspis, Discolobium, Adesmia, Chapmannia, Stylosanthes, Arachis, Zornia, Ougeinia, Desmodium, Mecopus, Pseudarthria, Pycnospora, Uraria, Lourea, Alysicarpus, Leptodesmia, Eleiotis, Hallia, Cranocarpus,* and *Lespedeza.*

[4] (1) Dalbergieae: species of *Dalbergia, Hecastophyllum, Machaerium, Drepanocarpus, Tipuana, Platypodium, Centrolobium, Pterocarpus, Poecilanthe, Platymiscium, Lonchocarpus, Derris, Pongamia, Piscidia, Muellera, Euchresta, Andira, Geoffroya, Dipteryx, Pterodon*; (2) Sophoreae: *Dalhousiea, Virgilia, Calpurnia, Cladrastis, Ammodendron, Sophora, Ormosia, Diplotropis, Bowdichia, Myrospermum, Myroxylon, Sweetia*; (3) Swartzieae: *Zollernia, Aldina, Swartzia.*

The **epidermis** of the leaf shows a series of different features, which may be employed for specific diagnosis. It is probably scarcely necessary to mention that within this large Order manifold differences occur in the character of the outer wall as regards thickness and in the nature of the lateral margins of the epidermal cells. With regard to the latter it may, moreover, be mentioned that lateral walls with angular folds, similar to those found in the petals of many plants, e.g. *Primula sinensis*, have been observed[1] by Köpff in *Euchresta Horsfieldii*, Benn., and *E. japonica*, Benth., and by Vogelsberger in some Hedysareae (*Coronilla emeroides*, Boiss. et Sprun., *C. Emerus*, L., *C. glauca*, L., and species of *Hippocrepis* and *Onobrychis*). Papillose differentiation of the epidermis of the leaf and gelatinization of its inner walls are widespread phenomena.

Typical papillose or subpapillose differentiation of the lower epidermis of the leaf has been observed: (*a*) among the Phaseoleae (according to Debold): in species of *Amphicarpaea, Camptosema, Clitoria, Erythrina, Glycine, Hardenbergia, Kennedya, Mucuna, Periandra, Pueraria, Shuteria*, and *Strongylodon*; (*b*) among the Galegeae (according to Weyland): in many Astragaleae and species of *Barbieria* and *Brongniartia*, many Coluteae, species of *Dalea, Diphysa, Harpalyce, Poitea*, and *Robinia*; (*c*) among the Hedysareae (according to Vogelsberger): in species of *Alysicarpus, Desmodium, Discolobium, Eleiotis, Geissaspis, Herminiera, Leptodesmia, Lespedeza, Lourea, Mecopus, Ougeinia, Pseudarthria, Pycnospora, Uraria*; (*d*) among the Dalbergieae (according to Köpff): in species of *Dalbergia, Derris, Drepanocarpus, Euchresta, Hecastophyllum, Lonchocarpus, Machaerium, Muellera, Myrospermum, Piscidia, Pterocarpus, Pterodon*; (*e*) among the Sophoreae and Swartzieae respectively (according to Köpff): in species of *Bowdichia, Calpurnia Cladrastis, Diplotropis*, and *Sophora, Swartzia*, and *Sweetia*; (*f*) among the Loteae: in species of *Lotus*, according to Vuillemin. Regarding the species concerned and the details of differentiation of the papillae, reference must be made to the original treatises. Papillose differentiation of the upper epidermis is rare, being present, e.g., in *Dalbergia pubescens*, Hook. f., according to Köpff, and in *Spartium junceum*, according to Reinke.

Nearly related to the papillae and connected with them by transitions are the cuticular projections observed by Reinke on both sides of the leaf in many Podalyrieae (species of *Brachysema, Daviesia, Eutaxia, Gastrolobium, Gompholobium, Oxylobium, Pultenaea*, and *Sphaerolobium*); they occur as solid and round or conical prominences of the middle part of the strongly thickened outer wall of the epidermal cells. Occasionally these structures are longer and are then like papillae or hairs (species of *Aotus, Chorizema, Dillwynia, Gastrolobium, Mirbelia, Oxylobium*, and *Sphaerolobium*).

Owing to the large number of species in which a mucilaginous epidermis has been demonstrated, usually only the genera concerned can be cited in the following list: (*a*) in the tribe Podalyrieae: *Aotus villosa*, Sm., *Brachysema lanceolatum*, Meissn., *Dillwynia ericifolia*, Sm., and *Gastrolobium villosum*, Benth., according to my own observations; (*b*) in the tribe Phaseoleae: species of *Atylosia, Camptosema, Canavalia, Clitoria, Cratylia, Cymbosema, Dioclea, Dolichos, Eriosema, Galactia, Kennedya, Periandra, Phaseolus, Rhynchosia, Rudolphia, Strongylodon*; (*c*) in the tribe Galegeae: species of *Amorpha, Brongniartia, Dalea, Diphysa, Petalostemon, Tephrosia*; (*d*) in the tribe Genisteae: *Genista tinctoria*, L., according to Walliczek, *Hovea pungens*, Benth., and *Bossiaea eriocarpa*, Benth., according to my own observations[2]; (*e*) in the tribe Hedysareae: species of *Adesmia, Aeschynomene, Arachis, Chaetocalyx, Chapmannia, Discolobium, Geissaspis, Herminiera, Nissolia, Ormocarpum, Pictetia, Poiretia, Smithia, Soemmeringia, Stylosanthes, Zornia*; (*f*) in the tribe Dalbergieae: species of *Andira, Dalbergia, Drepanocarpus, Piscidia, Platymiscium, Platypodium, Poecilanthe, Pterocarpus*; (*g*) in the tribe Sophoreae: species of *Ammodendron, Bowdichia, Cladrastis, Sophora*; (*h*) in the tribe Swartzieae: species of *Swartzia* and *Sweetia*.

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[1] The systematic significance of this feature for characterizing species requires further investigation. Thus Russell (loc. cit., 1895, p. 341 and pl. xvi, Fig. 10) also met with this feature on the lower side of the leaf of *Lotus corniculatus*, L., but in this case not constantly.

[2] In the two species last named the mucilaginous epidermis of the leaf was described by Reinke (loc. cit.) as a two-layered epidermis.

Development of **hypoderm** is not very widely distributed in the Order. The hypoderm is usually one-layered, more rarely two-layered, and is either developed on both sides of the leaf, or only on the upper or lower side. Gelatinization of the hypoderm-cells has been observed by Köpff in *Dalbergia Amerimnum*, Benth., *D. Sissoo*, Roxb., *Pterocarpus ancylocalyx*, Benth., and *Sophora tetraptera*, Ait.

Hypoderm is stated by Köpff and Debold to occur on the upper side of the leaf in the following species: *Andira Amazonum*, Mart.; *Canavalia altissima*, Macf.; *Cratylia floribunda*, Benth.; *Dalbergia Amerimnum*, Benth., *D. Sissoo*, Roxb.; *Diplotropis brasiliensis*, Benth.; *Hecastophyllum amazonicum*, Radlk., *H. Brownei*, Pers., *H. negrense*, Radlk.; *Lonchocarpus spiciflorus*, Mart.; *Myrospermum frutescens*, Jacq.; *Myroxylon peruiferum*, L. f.; *Sophora tetraptera*, Ait.; *Zollernia falcata*, Nees, *Z. ilicifolia*, Vog., *Z. splendens*, Nees. Hypoderm is described by Köpff as occurring on the lower side of the leaf in: *Andira spinulosa*, Mart.; *Bowdichia nitida*, Spruce, *B. virgilioides*, H.B.K. var.; *Geoffroya spinosa*, Jacq.; *Pterocarpus Hayesii*, Hemsl., *P. Rohrii*, Vahl;—by Köpff on both sides of the leaf in: *Pterocarpus ancylocalyx*, Benth., and *P. Rohrii*, Vahl var.; according to Reinke, a one-layered hypoderm is also found all round the phyllode-like leaves of species of *Daviesia*, e.g. *D. incrassata*, Sm. Lastly, Köpff notes the presence of tissue, resembling hypoderm, on the lower side of the leaf of species of *Centrolobium*, *Pterocarpus*, *Swartzia*, and *Sweetia*.

In connexion with the hypoderm it may be mentioned that the epidermal cells are secondarily divided by thin vertical walls in certain species of some genera (*Andira*, *Centrolobium*, *Dalbergia*, *Dipteryx*, *Geoffroya*, *Hecastophyllum*, *Platypodium*, *Poecilanthe*, *Pterodon*).

The **stomata** do not belong exclusively to one and the same type (Cruciferous type), as has hitherto been generally assumed (see Strasburger, loc. cit., and De Bary, loc. cit., p. 44). The type with subsidiary cells parallel to the pore (Rubiaceous type) is also very widely distributed. The following plants conform to the latter type: the Phaseoleae investigated by Debold; of the Galegeae, according to Weyland, only *Milletia* and *Psoralea*; of the Hedysareae, according to Vogelsberger: *Alysicarpus*, *Arachis*, *Cranocarpus*, *Desmodium*, *Discolobium* (? cf. loc. cit., pp. 11 and 42), *Eleiotis*, *Geissaspis*, *Hallia*, *Leptodesmia*, *Lespedeza*, *Lourea*, *Mecopus*, *Ougeinia*, *Pseudarthria*, *Pycnospora*, *Uraria*; of the Papilionaceae investigated by Köpff: the whole of the Dalbergieae excluding *Euchresta*, *Platymiscium*, and *Pterocarpus Hayesii*, Hemsley, all the Swartzieae except *Zollernia*, and finally, of the Sophoreae, only *Bowdichia*, *Dalhousiea*, *Diplotropis*, and *Ormosia*. In the following cases, on the other hand, the stomata are surrounded by three or more neighbouring cells: in the Galegeae investigated by Weyland, apart from the genera *Milletia* and *Psoralea* cited above; in most of the Hedysareae examined by Vogelsberger, but excluding *Alysicarpus*, &c. (see above), and according to Köpff, in most of the Sophoreae with the exception of *Bowdichia*, &c. (see above), as well as in *Pterocarpus Hayesii*, *Euchresta*, *Platymiscium*, and *Zollernia*, and lastly, according to Strasburger, in *Scorpiurus*. It is probably unnecessary to enter further into the fact that the stomata vary with regard to their position at or below the level of the epidermal cells (in the latter case occasionally in connexion with the formation of a deep chimney-like depression), and that they either occur on both sides of the leaf or only on the lower side. Only a few other special features deserve notice, and will now be mentioned. In the fairly large pinnules of *Geoffroya spinosa*, Jacq., the stomata, curiously enough, occur only on the upper side, no explanation of this being possible at present. On the other hand, the restriction of the stomata to the upper side in the more or less upwardly directed acicular leaves of *Dillwynia ericifolia*, *Pultenaea aristata*, *P. echinula*, *Celidium ciliare*, and *C. Vogelii*, according to Reinke, is scarcely surprising. In the phylloclades of *Carmichaelia australis*, R. Br., the

stomata lie parallel to one another and at the same time transverse to the longitudinal direction of the phylloclade. The stomata on the thorny branches of *Alhagi* (according to Schube) have the same transverse position, while in the branches of *Viminaria* the stomata, which are likewise parallel to one another, have the direction of the pore coincident with the direction of elongation of the branch. Groups of stomata are stated by Köpff to occur on the leaves of *Euchresta Horsfieldii*, Benth., and *E. japonica*, Benth.

The differentiation of the **mesophyll**, as one would expect, is very diverse, especially in the Podalyrieae, in which ericoid forms of leaf, such as rolled leaves, &c., occur (see Reinke, loc. cit.). A feature worthy of note is the occurrence of a special layer, characterized both by the shape of its cells and by their contents, in the middle of the mesophyll; this is what is called a middle layer [1]. It is always poor in chlorophyll and is frequently filled with tanniniferous contents, which are brown in the dried leaf. This middle layer is very widely distributed among the Phaseoleae; it occurs in species of *Atylosia*, *Butea*, *Calopogonium*, *Camptosema*, *Cajanus*, *Canavalia*, *Cleobulia*, *Cologania*, *Cratylia*, *Cylista*, *Cymbosema*, *Dioclea*, *Dolichos*, *Dunbaria*, *Eriosema*, *Erythrina*, *Fagelia*, *Flemingia*, *Galactia*, *Glycine*, *Hardenbergia*, *Kennedya*, *Periandra*, *Phaseolus*, *Physostigma*, *Pueraria*, *Rhynchosia*, *Rudolphia*, *Spatholobus*, and *Teramnus*. Among the Galegeae, Weyland met with the middle layer in the genera *Coursetia*, *Cracca*, *Halimodendron*, *Indigofera*, *Mundulea*, and *Tephrosia*; among the Hedysareae, Vogelsberger found it in the genera *Alysicarpus*, *Desmodium*, *Eleiotis*, *Leptodesmia*, *Lespedeza*, *Mecopus*, *Ougeinia*, *Pseudarthria*, and *Pycnospora*; and lastly Köpff found it in species of *Derris*, *Lonchocarpus*, *Muellera*, and *Pongamia*. On the other hand, in the leaves of *Chapmannia floridana*, Torr. et Gray, and of species of the genera *Arachis*, *Cranocarpus*, and *Stylosanthes*, the lowest layer of the spongy parenchyma consists of cells with wide lumina and brown contents (in the dried leaf). Another character of the mesophyll, which is much less widely distributed, is afforded by the occurrence of sclerenchyma-fibres running free in this tissue. The following species show this: *Ammodendron Karelinii*, Fisch. et Mey., *Andira Amazonum*, Mart., *Bowdichia nitida*, Spruce, *Ormosia excelsa*, Spruce, *O. polyphylla*, Herb. Monac. (Spruce, No. 1194), *Platymiscium nitens*, Vog., *Swartzia apetala*, Raddi, and *S. acuminata*, Willd. Branched spicular cells are mentioned by Köpff in *Swartzia Benthamiana*, Miq., and *S. rosea*, Mart. Lastly, mucilaginous mesophyll-cells occur in *Petalostemon candidus*, Michx., *P. gracilis*, Nutt., and *P. violaceus*, Michx.

The structure of the **veins** of the leaf presents varied features. Apart from the occurrence or absence of a sclerenchymatous sheath to the vascular bundles of the veins it is noteworthy that the smaller bundles are either vertically transcurrent, reaching as far as the upper and lower epidermis by means of tissue which may have thin walls or be sclerenchymatous, or they are embedded. I omit more detailed accounts of the material investigated from this point of view, and refer to the works of Debold, Weyland, Vogelsberger, and Köpff, cited below.

Of **internal glands**, the most widely distributed are tubular, elongated cells (reaching ·5 mm. in length), which are characterized by their wide lumina (Fig. 56), and are described in the literature as tannin-sacs [2] on account of their contents, which are usually rich in tannin and are mostly brown in dried material. Since these elements were first investigated by Sachs in *Phaseolus*,

[1] The colourless centrally placed medullary tissue in the leaf of many Podalyrieae and Genisteae (Reinke) is not identical with this middle layer.

[2] The terms laticiferous tubes ('Milchröhren') used by Taubert, and canals ('Gänge') used by Schenck (Aërenchym, loc. cit.) for *Sesbania* are not correct.

and since Trécul for the first time pointed out their frequent occurrence in the Order, their nature, contents, and distribution have repeatedly formed the subject of investigation. They are for the most part simply cells; in other cases an origin by means of fusion is certain, according to the concordant investigations of Avetta, Borzi, Baccarini, and Weyland. According to Russell the sacs (apart from those of the secondary bast) originate very early at the growing point of the axis, before the wood and bast become differentiated. They occur in relation to the vascular system, and in the axis are found united into groups at the margin of the pith, in the outer part of the bast internal

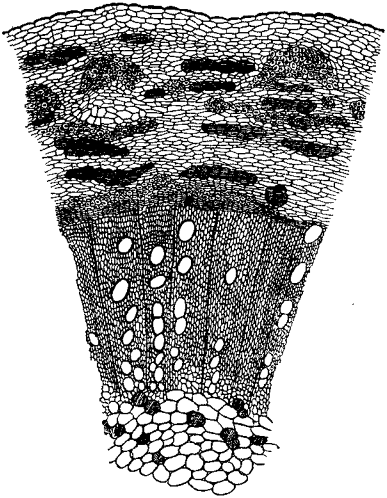

FIG. 56. Transverse section through the axis of ***Machaerium secundiflorum***, Mart., with wide-lumened tannin-sacs (which are shaded in the figure) in the pith, bast and primary cortex.—Original.

to the primary hard bast, or between the primary bundles of hard bast, or in the secondary bast, occasionally also in the primary cortex; they may be followed from the branch into the corresponding tissues of the veins of the leaf. From the investigations described in detail below it appears that the contents, which in the living plant are under considerable pressure, are usually tanniniferous, but vary in other respects, and are specially often rich in proteid-substances.

The sacs in question mostly have tanniniferous contents, which in the living plant are colourless, but become brown through the action of oxidizing reagents, such as *eau de Javelle*, and likewise through the drying of the plant, if sufficient time is allowed. Now and then, however, the contents are poor in tannin or destitute of it, and resemble latex in the living plant (in ***Apios tuberosa, Sesbania***, and ***Vigna glabra***, according to Trécul, and in ***Lablab vulgaris***, according to Haberlandt).

Apart from tannin, according to Baccarini, proteid-substances and different kinds of sugar are the essential components of the contents; an accumulation of proteid is stated to occur first in the sacs, and then the tannin appears, if at all. Even though Baccarini's proteid-reactions are not quite free from objection, still the aggregation-phenomena, obtained by Weyland by means of coffeïn- and antipyrin-solution, indicate, according to Löw and Bokorny, the storing up of large quantities of albumen. The contents of the sacs, however, may also occasionally resemble kino. Debold has proved this by macroscopic investigation of the contents, which exuded in considerable quantity on cutting a stem of *Spatholobus*, and became oxidized so as to form brown crusts; the same was done by Höhnel, who proved that the kino derived from *Pterocarpus Marsupium*, Roxb. comes from the secretory sacs in question.

It may be added that the same contents as are found in the sacs are occasionally also present in mesophyll-cells, which are either of special shape or scarcely different from the remaining cells. They are particularly often found in a middle layer of the mesophyll (see above). In these cells the characteristic contents often only appear inconstantly ('transitory' and 'definitive' secretory sacs of Baccarini).

The following review gives the general outlines of the distribution of the tannin-sacs, &c., in the Papilionaceae; it may be mentioned at once that the tannin-sacs do not generally occur in all, but only in certain species of the same genus.

(*a*) Podalyrieae and Genisteae (little investigated; tannin-sacs): only in the 'pith' of the phyllode-like leaves of *Daviesia incrassata*, Sm. (my own observation). (*b*) Trifolieae: tannin-sacs in *Melilotus*, but imperfectly differentiated (Baccarini). (*c*) Loteae: tannin-cells in the mesophyll of *Lotus* (Volkens, Vuillemin), in the branch (according to Trécul) in *Anthyllis* and *Securigera* (pith), *Hosackia* (pith and primary cortex), *Lotus* (between the primary groups of hard bast), *Dorycnium* and *Tetragonolobus* (pith and between the primary groups of hard bast). (*d*) Phaseoleae: according to Debold, tannin-sacs in the pith and bast in *Apios, Atylosia, Butea, Cajanus, Calopogonium, Camptosema, Canavalia, Centrosema, Cleobulia, Clitoria, Cochlianthus, Cologania, Cratylia, Cylista, Cymbosema, Dioclea, Dolichos, Dunbaria, Eriosema, Fagelia, Flemingia, Galactia, Grona, Hardenbergia, Kennedya, Mucuna, Periandra, Phaseolus, Platycyamus, Pueraria, Rhynchosia, Shuteria, Spatholobus, Teramnus*, and *Vigna*, only in the bast in *Amphicarpaea, Dumasia, Erythrina*, and *Strongylodon*; according to Trécul[1] tannin-sacs on the inner side of the primary hard bast in *Dolichos*, in the pith and primary cortex in *Dolichos* and *Erythrina*, in the pith and on the inner side of the primary hard bast in *Amphicarpaea, Dolichos* (*Lablab*), *Fagelia, Phaseolus, Kennedya*, and *Rhynchosia*. (*e*) Galegeae: according to Weyland (1) short, isodiametric tannin-cells in the middle layer of the leaf in *Indigofera, Petalostemon*, and *Tephrosia*, in the spongy tissue in *Corynella, Olneya, Poitea, Robinia, Sabinea, Wistaria*, and in the palisade-tissue in the form of enlarged palisade-cells in *Calophaca, Caragana, Corynella, Glycyrrhiza, Halimodendron, Olneya, Poitea, Robinia, Tephrosia*, and *Wistaria*; (2) tannin-sacs, accompanying the primary hard bast, in *Amorpha, Eysenhardtia, Glycyrrhiza, Indigofera, Lessertia, Milletia, Petalostemon*, and *Psoralea*, and in the pith in *Amorpha, Corynella, Coursetia, Dalea, Glycyrrhiza, Harpalyce, Indigofera, Milletia, Mundulea, Olneya, Petalostemon*, and *Robinia*; according to Trécul[1], tannin-sacs in the primary cortex in *Dalea*, on the inner side of the primary hard bast in *Psoralea*, in the pith and primary cortex in *Calophaca* and *Dalea*, in the pith and on the inner side of the primary hard bast in *Amorpha, Eysenhardtia, Glycyrrhiza, Robinia, Sesbania* (*Daubentonia*) and *Wistaria*. (*f*) Hedysareae: according to Vogelsberger and others, special idioblasts, filled with brown contents, frequently present in the mesophyll (in *Scorpiurus* in the whole of the mesophyll, in *Alhagi, Coronilla, Ebenus, Eversmannia, Hedysarum*[2], *Onobrychis, Ormocarpum, Ornithopus*, and *Taverniera* immediately beneath the upper and lower epidermis); quite similar elements are not uncommon in the primary cortex, forming the subepidermal layer of cells (*Alhagi* according to Schube, *Taverniera aegyptiaca*, Boiss. according to Volkens, almost all the Euhedysareae according to Vogelsberger); tannin-sacs in the axis, according to Vogelsberger in the pith in the Coronilleae, Euhedysareae, Aeschynomeneae (excl. *Chaetocalyx*), Adesmieae,

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[1] Trécul's statements are quoted separately, because it does not clearly appear from them, how wide his interpretation of the term 'tannin-sacs' was.

[2] To this category also belong the secretory cells with brown contents, mentioned by Bokorny in *Hedysarum Mackenzii*, Rich.

Stylosantheae, in *Ougeinia*, *Desmodium*, *Pseudarthria*, *Leptodesmia*, and *Lespedeza*, in the soft bast in *Hammatolobium*, *Eversmannia*, *Alhagi*, and the Desmodieae (excl. *Cranocarpus*), between the primary groups of bast-fibres in *Chapmannia*, *Desmodium*, *Discolobium*, *Ebenus*, *Eversmannia*, *Hedysarum*, *Leptodesmia*, *Onobrychis*, *Ornithopus*, and *Taverniera*, in the primary cortex in *Hedysarum* and *Alhagi*, frequently also (e.g. in most of the Aeschynomeneae, some Stylosantheae, &c.) accompanying the vascular bundles of the veins, and now and then (*Hallia*) also in the neighbourhood of the veins; according to Trécul (see previous foot-note), tannin-sacs in the pith in *Adesmia*, *Arachis*, *Coronilla*, *Hippocrepis*, *Nissolia*, *Ornithopus* (*Arthrolobium*) and *Zornia*, on the inner side of the primary hard bast in *Uraria*, in the pith and primary cortex in *Adesmia*, *Scorpiurus*, and *Stylosanthes*, in the pith and between the primary hard bast in *Hedysarum*, *Onobrychis*, and *Ornithopus*, in the pith, between the primary hard bast and on the inner side of the latter in *Hedysarum*, *Onobrychis*, and *Ornithopus*, in the pith and on the inner side of the primary hard bast in *Desmodium*. (*g*) Dalbergieae: tannin-sacs, according to Köpff, in *Andira*, *Centrolobium*, *Dalbergia*, *Derris*, *Dipteryx*, *Drepanocarpus*, *Geoffroya*, *Lonchocarpus*, *Machaerium*, *Muellera*, *Piscidia*, *Platypodium*, *Poecilanthe*, *Pongamia*, *Pterocarpus*, *Tipuana*. (*h*) Sophoreae: tannin-sacs, according to Köpff, in *Bowdichia*, *Diplotropis*, *Ormosia* and *Sweetia*. (*i*) Swartzieae: tannin-sacs, according to Köpff, in *Aldina* and *Swartzia*.

A second category of internal glands is formed by secretory cells with different (viz. mucilaginous or resinous) contents, which do not include tannin and are therefore not coloured brown in dried material. These cells have been observed in certain Galegeae (*Mundulea*, *Tephrosia*), Hedysareae (*Hallia*), Dalbergieae (*Lonchocarpus*, *Machaerium*, *Muellera*, *Pongamia*), and Sophoreae (*Sophora*).

The secretory cells of the following genera of Galegeae—*Mundulea* (*M. suberosa*, Benth.) and *Tephrosia* (*T. candida*, DC., *T. capensis*, Pers., *T. cinerea*, Pers., *T. dichroocarpa*, Steud., *T. grandiflora*, Pers., *T. nubica*, Bak., *T. tinctoria*, Pers.)—have resinous contents and occur in the mesophyll, as well as in the tissues of the axis. In *Mundulea suberosa* the resin-cells contain a protoplasmic network, in the meshes of which resin is stored up. The secretory cells of the genus *Hallia* (*H. alata*, Thunb., *H. asarina*, Thunb., *H. cordata*, Thunb., *H. flaccida*, Thunb., and *H. imbricata*, Thunb.), belonging to Hedysareae, likewise have resinous contents, are situated just beneath the epidermis of the leaf, and are bounded on the inner side by narrow cells resembling an epithelium. Within the genus *Machaerium*, belonging to the Dalbergieae, the secretory cells are only present in one species, *M. longifolium*, Benth., where they have a flask-like form and belong to the epidermis of the leaf; they only contribute to the formation of the surface of the leaf as regards a relatively small part of their surface; their larger ventricose portions penetrate into the mesophyll; they also produce transparent dots in the leaf. Their contents are of the nature of gummy mucilage. The same kind of secretory cells as are found in *Machaerium longifolium* have been observed by Köpff in the Sophoreae, namely in some of the species of *Sophora* investigated by him (viz. *S. alopecuroides*, L., *S. angustifolia*, S. et Z., *S. flavescens*, Ait., *S. glauca*, Leschen., *S. Griffithii*, Stocks, *S. japonica*, L., *S. macrocarpa*, Sm., *S. pachycarpa*, C. A. Mey., and *S. tomentosa*, L.). Lastly, secretory cells are stated to occur in the pith of *Lonchocarpus latifolius*, H.B.K., *Muellera moniliformis*, L.f. and *Pongamia glabra*, Vent.

Secretory cavities form the third type of internal secretory receptacles. They have been observed in the tribe Galegeae in all the genera, forming the sub-tribe Psoraleae (*Amorpha*, *Apoplanesia*, *Dalea*, *Eysenhardtia*, *Marina*, *Petalostemon*, and *Psoralea*), and in *Milletia*, in the tribe Hedysareae in *Amicia*, *Poiretia*, and *Zornia*, in the tribe Dalbergieae in *Derris*, *Dipteryx*, *Lonchocarpus*, *Muellera*, *Piscidia*, *Pongamia*, and *Pterodon*, and in the tribe Sophoreae in *Myrospermum* and *Myroxylon*. In most cases they cause transparent dots in the leaf, and are usually characteristic of the genera concerned.

As to the detailed structure of the secretory cavities the following additional facts should be mentioned with regard to some of the genera cited—in the first place, those belonging to the tribe Galegeae. The intercellular secretory

receptacles of the Psoraleae (except *Psoralea*), according to Weyland, occur principally in the spongy tissue close below the epidermis of the leaf, and are bounded towards the mesophyll by a protective sheath of cells, which have thick walls and fit closely together. Inside this protective sheath a thin-walled epithelium is found in *Petalostemon*; this indicates the schizogenous origin of the secretory cavities. The secretory receptacles of *Dalea* and *Eysenhardtia* show a similar epithelium in the young leaf; in these plants, however, accordiug to Weyland, the epithelium subsequently becomes absorbed. According to the same author (and contrary to Höhnel), the secretory cavities of the genus *Amorpha* have a similar origin, except that in this case it is not an epithelial layer but an entire spherical mass of cells that becomes absorbed from within outwards, until the protective sheath mentioned sets a limit to the extension of the gland.

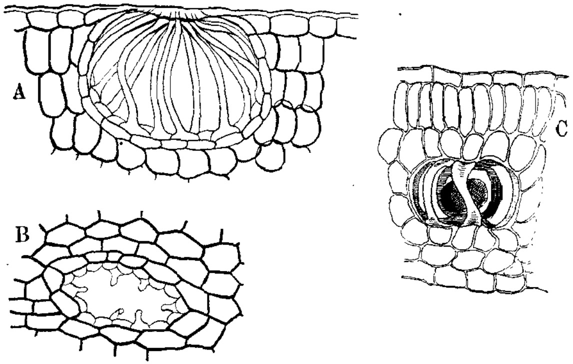


FIG. 57. A, Transverse section through an intramural gland of the leaf in *Psoralea hirta*, L. B, Transverse section through a secretory cavity in the primary cortex of *Lonchocarpus Spruceanus*, Benth., characterized by the papillose differentiation of the epithelium. C, Peculiar secretory cavity of *Lonchocarpus Spruceanus* with bracket-epithelium.—Original.

The genus *Psoralea* possesses peculiar intercellular secretory receptacles, viz. intramural glands. According to De Bary, these arise by an epidermal cell, which is arched towards the interior of the leaf, becoming divided by walls placed at right angles to the surface of the epidermis. The cells thus produced become strongly elongated in the same direction and at first form a hemisphere of cells, penetrating into the mesophyll, while their lateral walls at first remain firmly connected with one another. During the elongation of these cells resin appears in the bounding surfaces of the lateral walls, at first as a narrow homogeneous intramural layer at the middle of the cells, forming transverse rings around the centrally placed gland-cells, but subsequently loosening the lateral surfaces of the gland-cells more and more from one another, so that the latter appear as if embedded in the mass of secretion. Hence, for example, the mature gland (Fig. 57, *A*) in a transverse section of the leaf, shows a space filled with secretion, which abuts on the surface of the leaf, and is traversed by a variable (often large) number of narrow tubular

cells, curved more or less like meridians, and contributing to the formation of the surface of the leaf with their small polygonal terminal surfaces. According to Weyland, the gland is bounded towards the mesophyll by a protective sheath, consisting of a layer of cells, which are united without interruption, flattened and provided with undulated lateral margins, fitting closely into one another (for the sake of greater firmness). The external walls of the gland-cells, which take part in the formation of the surface of the leaf, are very considerably thickened. Moreover, the glands are not differentiated in the same manner in all the species of *Psoralea*. Occasionally (*P. Onobrychis*, Nutt.) they remain at a lower stage of development, in so far as no complete separation of the lateral walls of the gland-cells takes place. In the mature gland the contents of the tubular cells is the same as in the intercellular spaces of the gland; but at first they contain clear, scarcely granular protoplasm and clear cell-sap.

The secretory cavities of the two Psoralean genera, *Apoplanesia* and *Marina*, have still to be investigated in detail; the presence of secretory cavities is only deduced from the fact that Bentham and Hooker mention transparently dotted leaves and that they belong to the Psoraleae. The intercellular secretory receptacles of the Galegeae, referred to above, do not, however, occur in the leaf only, but also in the branch. In certain species of *Dalea*, e.g. *D. Emoryi*, Gray, *D. polyadenia*, Torr., and *D. spinosa*, Gray, they form lumps on the young branches.

Of the remaining genera cited above, belonging to the tribes Hedysareae, Dalbergieae, and Sophoreae, and characterized as a whole by the possession of schizogenous secretory cavities, species of the genera *Myrospermum*, *Piscidia*, *Lonchocarpus*, *Derris*, and *Pongamia* still require special discussion; in connexion with the two genera last named, the secretory receptacles of the genus *Milletia*, which is placed in the Galegeae by Bentham and Hooker, may also be considered in detail. The secretory cavities of *Myrospermum frutescens*, Jacq., which were wrongly interpreted by Bokorny, and which give rise to transparent dots and striae in the leaf, have peculiar contents, consisting of resin-grains, between which strands of proteid-like substance are united to form a framework resembling cellular tissue. According to Köpff, the secretory cavities present in the leaf of *Lonchocarpus glabrescens*, Benth. and *Piscidia Erythrina*, L., as well as in the primary cortex of *Lonchocarpus Spruceanus*, Benth. (Fig. 57, *B*), *L. glabrescens*, Benth., *Derris robusta*, Benth., and *D. scandens*, Benth., are rendered remarkable by the finger-like papillose differentiation of their epithelial cells. Still more noteworthy, however, is the occurrence of peculiar intercellular secretory receptacles (Fig. 57, *C*) in certain species of the genera *Lonchocarpus* and *Derris*; at first sight they have a strange appearance, but on closer examination they can be referred to the schizogenous secretory cavities. In the spongy parenchyma of a series of species of the genera *Lonchocarpus* and *Derris* approximately spherical spaces are to be observed in all or in some of the meshes of the veins; these are filled with a secretion, and are enclosed by a loose sheath of several bracket-shaped cells. These cells, which are curved like meridians, broaden out and meet at two poles, of which one is directed towards the upper side of the leaf and touches the palisade-tissue, while the other is turned towards the lower side of the leaf, and borders on the cells of the spongy parenchyma or projects freely into the lacunae of the latter. An aggregate of bracket-cells of this kind, which incompletely encloses the masses of secretion, may quite well be brought into relation with schizogenous secretory cavities, if one imagines the epithelium of the latter as being in the first place formed of tubular cells, which are curved like meridians, and united at the two poles, and if it also be assumed that the cells thus constituted are not firmly united together, but that their lateral contiguous walls become loosened from one another. The fact that both kinds of secretory elements are

occasionally to be observed side by side in the same species throws further light on the genetic relation between the secretory masses enveloped by bracket-cells and the ordinary schizogenous secretory cavities. Among the species of the genus *Lonchocarpus*, *L. glabrescens*, Benth., *L. praecox*, Mart., *L. subglaucescens*, Mart., and *L. violaceus*, H.B.K., according to Köpff, have the ordinary secretory cavities with non-lacunar epithelium in their leaves, while *L. campestris*, Mart., *L. denudatus*, Benth., *L. latifolius*, H.B.K., *L. rariflorus*, Mart., and *L. Spruceanus*, Benth., have secretory spaces enveloped by bracket-cells; in the axis (in the primary cortex alone or also in the pith) ordinary secretory cavities are present in all the above species with the exception of *L. campestris* and *L. denudatus*, in which Köpff did not observe any secretory organs in the axis. Concerning the species of *Derris*, investigated by Köpff, it may first be mentioned that in *D. negrensis*, Benth., *D. sinuata*, Benth. and *D. thyrsiflora*, Benth. no intercellular secretory organs have been observed. The rest of the investigated species of *Derris* (*D. cuneifolia*, Benth., *D. ferruginea*, Benth., *D. Heyneana*, Benth. var. *marginata*, Benth., *D. polystachya*, Benth., *D. robusta*, Benth., *D. scandens*, Benth. and *D. uliginosa*, Benth.) have masses of secretion, enclosed by bracket-cells in their leaves, while in some cases, namely in *D. cuneifolia*, *D. ferruginea*, *D. polystachya*, and *D. robusta*, ordinary secretory cavities with closed epithelium have also been observed in the strengthening tissue of the larger veins of the leaf. The latter cavities are usually also to be found in the axis of the species of *Derris* (in the primary cortex and in part also in the pith). Finally the same kind of secretory cavities, enclosed by bracket-cells, also occur according to my own observations in *Pongamia glabra*, Vent., and according to the statements of Radlkofer and Weyland in all investigated species of *Milletia* (*M. auriculata*, Bak., *M. cinerea*, Benth., *M. pachycarpa*, Benth., *M. Piscidia*, W. et A. and *M. splendens*, W. et A.). In the species of *Milletia* they are found only in the leaf at the boundary of the palisade and spongy parenchyma; with the upper ends of the bracket-cells, which meet at one pole, a tuft-like group of palisade-cells, evidently serving as collecting-cells, is often connected. In the axis of *Milletia* secretory masses enclosed by bracket-cells are absent; intercellular secretory organs in the axis are only present in *Milletia auriculata*, Benth., and occur in the form of schizogenous resin-canals. It may at once be added that schizogenous balsam-canals are only known in one other case among the Papilionaceae, viz. in *Myroxylon Pereirae*, Klotzsch, according to Mezger; in this plant they are situated in the primary cortex.

In connexion with the description of the secretory cells, secretory cavities and resin-canals the following points still require a brief consideration: viz. the gum-canals in the wood of *Herminiera Elaphroxylon*, Guill. et Perr., the formation of tragacanth in the species of *Astragalus* and the occurrence of indigo. According to the statements of most of the authors who have concerned themselves with the interesting structure of the wood of 'ambatsch,' the gum-canals of *Herminiera* only appear in the older xylem, being placed vertically in the wood and horizontally in the medullary rays. According to these authors, they arise secondarily in a lysigenous manner by gelatinization of groups of cells. When the gum-canals become empty, canals containing air remain in their place. Vogelsberger's observations are not quite in agreement with the above; he was able to observe the formation of the gum-canals of *Herminiera* in branches collected by Schweinfurth and belonging to the Herb. Monac. According to him the gum-canals are derived from groups of cells, the walls of which are strongly swollen, so that only quite a small lumen is left, though remains of protoplasm can still be recognized. According to Vogelsberger these altered groups of cells do not arise secondarily in the xylem-mass, but the metamorphosis commences in the cambium and the metamorphosed groups only become secondarily enclosed in the mass of wood.

Vogelsberger's observation, however, does not exclude the possibility that secondary gum-canals may also arise in the older wood in the manner described by the other authors. The formation of tragacanth in the species of *Astragalus* was first correctly interpreted by Mohl, and was described by him in the case of numerous species. The metamorphosis begins at the centre of the pith. The thin cell-walls of this tissue become gradually thickened and swell up at the same time, while a stratification of the membranes becomes visible. Later on the stratification disappears and the cell-wall becomes converted into a homogeneous jelly. Subsequently the cells of the medullary rays also take part in the formation of gum. Besides this gummose alteration of the pith, Weyland met with dense, transparent contents in the cells of the periphery of the pith, of the primary cortex, and of the medullary rays in *Astragalus brachy-*

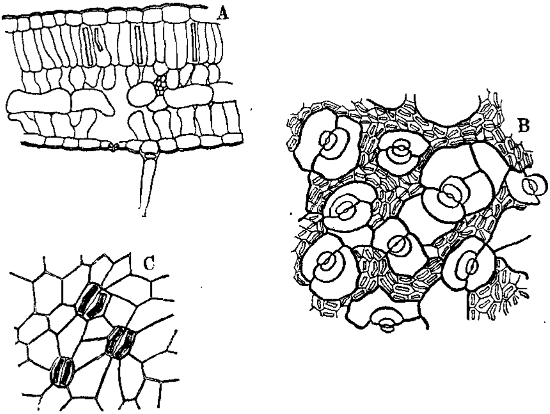


FIG. 58. A, Transverse section of the leaf of *Rhynchosia rufescens*, DC. with styloid-like crystals in the palisade-tissue. B, Surface-view of the epidermis of the leaf of *Stylosanthes procumbens*, Sw. C, Twin crystal-containing cells in the epidermis of the leaf of *Canavalia villosa*, Benth.—Original.

calyx, Fisch. (Herbarium-material!); these contents are surrounded by the primordial utricle, stain blue with watery iodine-solution, and are consequently of an amyloid-like nature. Finally, Weyland was able to demonstrate the presence of indigo microchemically (decolorization by reduction with alkaline solution of grape-sugar and blue coloration by oxidation after washing out with water and exposure to the air) in the leaves of *Petalostemon*; indigo, as is well known, also occurs elsewhere in the Order (*Indigofera*, &c.).

According to Borodin and other observers, the mode of excretion of **oxalate of lime**[1] is very characteristic. Oxalate of lime occurs almost exclusively in the form of solitary crystals, which have either the ordinary

[1] Occasionally crystalline elements are completely absent, e.g. according to Weyland in the allied genera, *Clianthus*, *Sutherlandia*, *Lessertia*, *Swainsona*, *Sphaerophysa* and *Colutea*; *Gueldenstaedtia*, *Astragalus* and *Oxytropis*.

rhombohedral shape, or that of small rods or styloids. Clustered crystals have only been observed in quite isolated cases; thus by Möller in the cortex of *Sophora japonica*, L. and by Vuillemin in the sepals of *Lotus*. Sphere-crystals of oxalate of lime have been met with by Vogelsberger in only one genus, namely in the mesophyll of *Discolobium hirtum*, Benth. and *D. pulchellum*, Benth.; small crystalline grains or prisms have been found by Köpff in the mesophyll of species of the genera *Dalbergia*, *Derris*, *Hecastophyllum*, *Virgilia*, and *Swartzia*, and small spherical crystalline bodies, consisting of oxalate of lime, by Weyland in the epidermal cells of *Dalea domingensis*, DC. Other characteristic modes of excretion of oxalate of lime, such as raphides or crystal-sand, are entirely wanting in the sub-order.

As regards the two forms of solitary crystals, the ordinary rhombohedra occur especially in the tissue accompanying the vascular bundles of the veins, in the chambered fibres of the bast and wood and also in the primary cortex; they are frequently embedded in thickenings of the walls of the cells which contain them. Those crystals which are rod-shaped or resemble styloids (see Fig. 58, *A*) are specially peculiar to the mesophyll (palisade-tissue), but occasionally occur in the epidermis of the leaf, in the crystal-containing chambered fibres of the bast and also accompanying the sclerenchyma of the veins. They are, strictly speaking, not solitary, but hemitropic crystals, consisting of two or more individual crystals arranged with their longitudinal axes in approximately the same direction, and consequently in certain positions they appear bent at one or more places. Not uncommonly, especially in the palisade-tissue, these rod-shaped crystals are embedded at one or at both ends in thickenings of the cell-wall and are surrounded by a film of cellulose.

Among the Phaseoleae Debold describes cells of the palisade-tissue, occupied by rod-shaped crystals as occurring in species of *Atylosia*, *Calopogonium*, *Canavalia*, *Centrosema*, *Cologania*, *Dioclea*, *Eriosema*, *Erythrina*, *Flemingia*, *Galactia*, *Glycine*, *Grona*, *Mucuna*, *Pachyrhizus*, *Phaseolus*, *Pueraria*, *Rhynchosia*, *Rudolphia*, *Spatholobus*, *Strongylodon*, *Teramnus*, and *Vigna*; Borodin describes the same in *Amphicarpaea* and *Clitoria*; Weyland among the Galegeae in species of *Coursetia*, *Dalea*, *Diphysa*, *Eysenhardtia*, *Harpalyce*, *Indigofera*, *Milletia*, *Olneya*, *Petalostemon*, *Peteria*, *Poitea*, *Psoralea*, *Robinia*, *Tephrosia*; Vogelsberger among the Hedysareae in species of *Aeschynomene*, *Arachis*, *Chapmannia*, *Coronilla*, *Hammatolobium*, *Herminiera*, *Lourea*, and *Pictetia*, and Borodin also in *Desmodium*; Köpff in species of the following genera of Dalbergieae,—*Dalbergia*, *Drepanocarpus*, *Geoffroya*, *Lonchocarpus*, *Machaerium*, *Muellera*, *Poecilanthe*, and *Pongamia*, of the Sophorean genus *Sophora*, and of the genera *Swartzia* and *Sweetia* of the Swartzieae; finally Borodin has also described them in species of *Eutaxia* (of the tribe Podalyrieae), *Orobus* (tribe Vicieae) and *Anthyllis* (tribe Loteae).

The occurrence of solitary crystals in the epidermis of the leaf is not rare, and is characteristic for the species concerned, and occasionally also for genera.

Among the Phaseoleae investigated by Debold mention may first be made of the genus *Canavalia* in this respect. All the investigated species of this genus are distinguished by the possession of characteristically arranged crystal-containing cells (Fig. 58, *C*). Hemitropic crystals, differentiated as small rods, occupy isolated pairs of cells, around which the other epidermal cells are grouped in a radial manner. In surface-view the two crystal-cells have a polygonal outline, and each is in contact with the other by a relatively long lateral wall, like the two guard-cells of a stoma; their lateral and inner walls are strongly thickened, the outer wall, on the other hand, is thin, and the lumen is filled by the crystal. Similar small crystal-cells, isolated or associated in groups, which vary in size but are less regular than in *Canavalia*, also occur in other genera of the Phaseoleae, but in these they are only of value in specific diagnosis; from this point of view the following species should be mentioned, according to Debold: *Cleobulia leiantha*, Benth.; *Cratylia floribunda*, Benth., *C. mollis*, Mart.; *Dioclea bicolor*, Benth., *D. glabra*,

Benth., *D. reflexa*, Hook. f.; species of *Dolichos*, not individually named; *Eriosema Benthamianum*, Mart., *E. cajanoides*, Hook. f., *E. longepedunculatum*, Rich.; *Erythrina indica*, Lam.; *Galactia Elliottii*, Nutt., *E. glabella*, Michx., *E. Martii*, DC., *E. Neesii*, DC.;—according to Borodin also: *G. cubensis*, H.B.K. and *G. tenuiflora*, W. et A.; *Glycine clandestina*, Wendl.; *Rudolphia rosea*, Tuss., *R. volubilis*, Willd. According to Weyland, crystal-cells of this kind, isolated or associated in groups, are also present in certain Galegeae. Where the crystal-cells occur in groups in the epidermis, they are distinguished from the remaining epidermal cells by their smaller size. In *Petalostemon* Weyland has shown developmentally that these groups are not produced by secondary division of one epidermal cell, but are epidermal cells which have been overgrown by their neighbours. In form the crystals in the Galegeae are shortly rod-shaped. Crystal-cells have been observed by Weyland in the epidermis of the leaf in the following species: *Dalea versicolor*, Zucc.; *Milletia cinerea*, Benth., *M. pachycarpa*, Benth.; *Petalostemon candidus*, Michx., *P. corymbosus*, Michx., *P. gracilis*, Nutt., *P. violaceus*, Michx. var.; *Psoralea bracteata*, L. var.;—likewise by Borodin in: *Dalea domingensis*, DC., *D. frutescens*, Gray; *Petalostemon carneus*, Michx., and *P. phleoides*, Torr. et Gray. Among the Hedysareae peculiar crystal-cells, showing a characteristic distribution, occur, according to Vogelsberger, in the epidermis of the leaf in species of the genus *Stylosanthes* (Fig. 58, *B*). These were first observed by Borodin, but were interpreted by him in an erroneous manner. The epidermis on both sides of the leaf in the species of *Stylosanthes* consists (*a*) of the stomatal apparatus, including the two to four subsidiary cells, which are placed parallel to the pore, and (*b*) apart from these, almost exclusively of extraordinarily numerous, flat, very small and low cells, which are polygonal in surface-view and have their inner walls strongly thickened, whilst their outer walls are thin and the lumen of each is filled by a short rod-shaped crystal. These crystal-cells in surface-view are grouped to form an extremely characteristic network, the meshes of which are occupied by the stomata with their subsidiary cells. As a rule, there is only one stoma in each mesh, occasionally several; in the latter case an ordinary, relatively large epidermal cell is frequently intercalated between the subsidiary cells. Below the crystal-cells on the upper side of the leaf (i. e. singly below a group of such cells) elongated cells occur, which taper conically downward, and have a mucilaginous lower membrane; in a similar manner hypodermal cells with large lumina, filled with brown contents, are found above the crystal-cells of the lower epidermis. These cells are thus present on both sides, and are perhaps of epidermal origin; they are placed so that the portion adjacent to the crystal-cells lies on the same level as those parts of the cells forming the stomatal apparatus, which are directed towards the interior of the leaf. Owing to this it appears on superficial examination as if the hypodermal cells were epidermal cells, in the strongly thickened outer membranes of which the crystals were embedded. Besides occurring in *Stylosanthes*, similar small crystal-cells, situated in the epidermis of the leaf, are found among the Hedysareae in *Arachis glabrata*, Benth., *A. hypogaea*, L., *A. prostrata*, Benth., *Cranocarpus Martii*, Benth., and *Chapmannia floridana*, Torr. et Gray; in these species they occur especially along the course of the veins—in *Chapmannia* singly, in *Arachis* mostly in pairs, in *Cranocarpus* in groups of from 2 to 10. Lastly, according to Köpff, epidermal cells occupied by rod-like crystals are likewise present among the Dalbergieae in *Drepanocarpus ferox*, Mart. and *Geoffroya spinosa*, Jacq., and in *Sophora speciosa*, Benth., *Swartzia Langsdorffii*, Raddi, and *S. Flemmingi*, Raddi.

Finally, one or two special modes of occurrence of oxalate of lime may be mentioned. The crystals occasionally attain considerable dimensions, e.g. according to Weyland, in the tissue accompanying the veins of the leaf in *Sabinea florida*, DC. and the two nearly allied genera *Harpalyce* and *Brongniartia*. Weyland observed a special arrangement of the crystals in the cortex of *Dalea polyadenia*, Torr., and in the leaf of *Indigofera lespedezioides* H.B.K. In the pericycle of *Dalea polyadenia* there are groups of crystal-cells which are elongated in the vertical direction, and have assumed the position and apparently also the physiological function of bundles of bast-fibres, which are here absent. The crystal-cells of the mesophyll of *Indigofera lespedezioides* have a similar mechanical significance; for here, below the base of the two-armed hairs, which are strongly incrusted with carbonate of lime, palisade-like

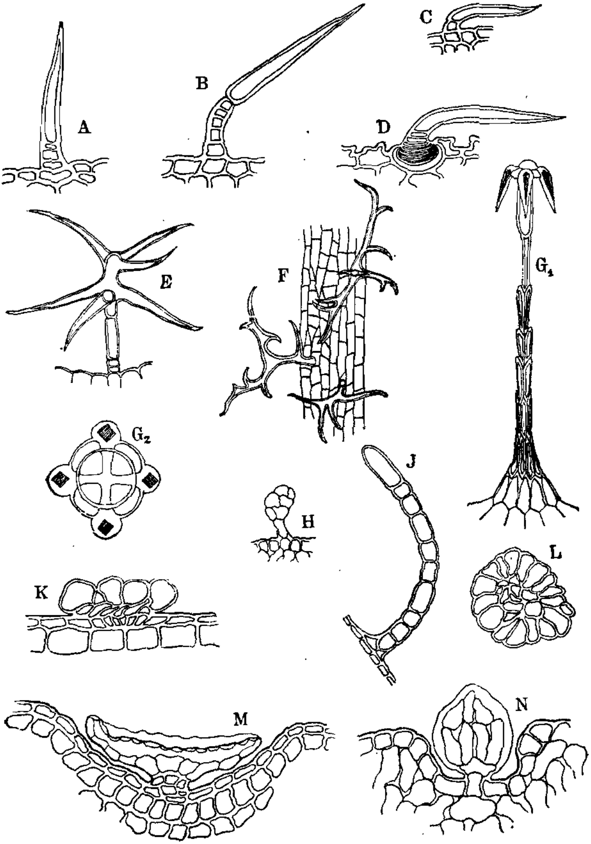
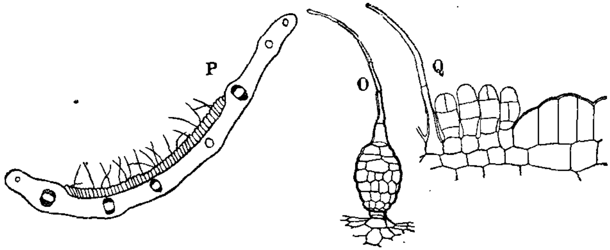


FIG. 59. Hairy covering of the Papilionaceae. A–C, Ordinary Papilionaceous hairs. D, Simple hair of *Lonchocarpus negrensis*, Benth., with bulbous septate base. E, Branched hair of *Erythrina indica*, Lam. F, Branched trichomes of *Dipteryx rosea*, Spruce. G_1, Anchor-like shaggy hair of *Cranocarpus Martii*, Benth.; G_2, Head of the anchor, seen from above. H, Glandular hair of the Phaseoleae. J, Uniseriate glandular hair of *Pongamia glabra*, Vent. K–L, Peltate glands of *Pterocarpus ancylocalyx*, Benth. M, Section through a peltate gland of *Centrolobium robustum*, Mart. N, External gland of the Phaseoleae. O, Bulbous hair of *Fagelia* P–Q, *Vicia Faba*; P, Transverse section through a stipule with its glandular area; Q, The glands of the glandular area strongly magnified.—A, B, C, D, J, K, L and M after Köpff; H, N after Debold; Q and R after Haberlandt; E, F, G_1, G_2 and O original.



cells occur; these are occupied by a prismatic crystal traversing the whole length of the lumen, and clearly serve as supports for the two-armed hairs.

The hairy covering (Fig. 59) consists of clothing and glandular hairs. The former may be subdivided into simple trichomes and shaggy hairs, according as they consist of a simple row of cells or of several rows. In almost all cases the simple hairs appear to be uniseriate, and at the least two-celled [1]. Ordinary unicellular hairs, which are widely distributed in both the other sub-orders of the Leguminosae—the Caesalpinieae and Mimoseae—are absent in the Papilionaceae. The scattered statements in the literature, with which I am acquainted, regarding the presence of trichomes of this kind have proved to be due to the small basal cells [2] having been overlooked. The ordinary simple hairs (Fig. 59, *A–C*) are distinguished by the fact that they consist of a row of two or several cells, of which in the first case the lower cell, in the second case all the cells except the terminal one, are strikingly short, being developed as basal cells, while the terminal cell alone is of considerable length; this cell varies in the structure of its wall and the size of its lumen, as well as in shape and direction. The form of hair just described is very widely distributed in the Phaseoleae, Galegeae, Hedysareae, Dalbergieae, Swartzieae, and Sophoreae, according to Debold, Weyland, Vogelsberger and Köpff; it also occurs in the Podalyrieae (*Anagyris, Gastrolobium, Podalyria argentea,* Salisb.), Genisteae (*Cytisus* and *Ulex,* according to Schube, *Genista,* according to Pirotta, *Lupinus, Retama*), Trifolieae (*Trifolium alpestre,* L.) and Loteae (*Lotus,* according to Vuillemin and Volkens) and Vicieae (*Vicia villosa,* Roth). It is out of place here to enter into further details as to the form and structure of these hairs. Only one or two prominent structural features found in some Papilionaceae require brief mention. According to Vogelsberger, in certain species of *Ebenus* the end-cell of the trichomes under discussion is provided with small tooth-like papillae [3], which are directed towards the apex of the hair. According to Köpff, in some Dalbergieae, Sophoreae, and Swartzieae (species of the genera *Andira, Diplotropis, Drepanocarpus, Lonchocarpus, Machaerium, Pterocarpus* and *Swartzia*) the basal cell, which lies in the plane of the epidermis, is enlarged and its upper portion subdivided by a large number

[1] I do not regard the papillae of certain Podalyrieae, which are developed like hairs (see above) as of that nature, especially as the characteristic uniseriate hairs of the Papilionaceae occasionally occur side by side with them, e.g. in *Gastrolobium villosum,* Benth.

[2] This is the case with the unicellular hairs, stated by Petit to occur in *Lupinus, Anagyris foetida* and *Cytisus Laburnum,* and with the trichomes of *Retama Raetam,* etc. drawn by Ross as unicellular.

[3] A similar structure has been observed by H. Schenck in *Medicago arborea, Clianthus puniceus* and *Onobrychis montana,* and by me in *Trifolium alpestre.*

of closely placed cell-walls, so that this series of cross-walls often projects convexly into the lumen of the lowermost basal cell, like a concentrically stratified cystolith (Fig. 59, *D*[1]). Lastly, the simple uniseriate trichomes of *Amicia zygomeris*, DC., depart from the typical form of the hair in question in the fact that their 3–5 cells are of approximately equal length. With these may be classed the club-shaped, uniseriate, articulated hairs consisting of a few cells of equal length with wide lumina, observed by Köpff in *Ormosia discolor*, Spruce and *O. macrophylla*, Benth.

Characteristic uniseriate forms of hairs belonging to the Papilionaceae also include two-armed hairs, branched hairs and hooked hairs or bracket-hairs. Two-armed hairs have been observed among the Phaseoleae in species of *Erythrina*, among the Galegeae in *Astragalus*, *Cyamopsis*, *Gueldenstaedtia*, *Indigofera*, *Lessertia*, *Sphaerophysa* and *Swainsona* among the Sophoreae in a species of *Diplotropis* of the section *Clathrotropis* (*D. nitida*, Benth.). They possess either one or two basal cells of variable length. The end-cell may have either thin or thick walls and is of varied shape. The arms may be either equal or unequal; in the latter case (which has been observed, e.g. in species of *Erythrina*, *Astragalus*, *Indigofera*, and *Swainsona*) transitions may occur to one-armed hairs, no arm being developed on one side, but only a rounded swelling (e.g. in *Gueldenstaedtia stenophylla*, Bunge). In the trichomes with equal arms the two ends may be pointed or blunt, or only one arm may be pointed and the other one like a flat-iron (*Sphaerophysa salsula*, DC., *Swainsona lessertiaefolia*, DC.). It occasionally happens that one of the arms forks, whereby the whole trichome comes to resemble a boot-jack (*Erythrina tomentosa*, R.Br.). The two-armed hairs of the genera of Galegeae are specially characterized by the fact that the thick wall of their end-cell is almost without exception incrusted with carbonate of lime. The carbonate of lime appears to be distributed throughout the membrane of the terminal cell, but in specially large quantity in the apices of the latter and in the wart- or peg-like thickenings which the end-cells of the two-armed hairs of the Galegeae not uncommonly exhibit. In two cases (in *Cyamopsis psoraloides*, DC., and *Indigofera lespedezioides*, H.B.K.) Weyland observed a central body, of the nature of a cystolith and incrusted with carbonate of lime, in the terminal cells. Branched hairs, consisting of a uniseriate stalk and a branched terminal cell, with the branches in two tiers, occur in *Erythrina indica*, Lam. (Fig. 59, *E*) and *E. velutina*, Willd., and in these species replace the two-armed hairs found in other species of the same genus; the branching of the terminal cell often resembles that of a fir-tree. Closely connected with the type of hair just described are the branched unicellular hairs (Fig. 59, *F*), already mentioned above, and described by Köpff in species of *Dipteryx* (*D. odorata*, Willd., *D. rosea*, Spruce and *D. tetraphylla*, Spruce); his illustration (Fig. 6, plate 1), which is intended to represent the branched hairs on the axis of *D. rosea*, does not, however, entirely agree with what I have found, the trichomes in this species being more like a stag's horn, with few or many branches. The hooked hairs consist of one or two, rarely more, short basal cells and a larger terminal cell bent into the form of a hook. They have been found in the following genera of Phaseoleae: *Canavalia*, *Centrosema*, *Clitoria*, *Periandra*, and *Phaseolus*; in the genus *Barbieria* of the Galegeae; and among the Hedysareae in the genera *Alysicarpus*, *Desmodium*, *Eleiotis*, *Leptodesmia*, *Lourea*, *Mecopus*, *Ougeinia*, *Pictetia*, *Pseudarthria*, *Pycnospora*, and *Uraria*.

Shaggy hairs, filiform multicellular structures, have been observed only

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[1] According to Haberlandt (Sitz.-Ber. Wiener Akad., Bd. ciii, Abt. 1, 1894, p. 518 et seq. and Ber. deutsch. bot. Gesellsch., 1894, p. 369) the trichomes of *Machaerium oblongifolium*, Vog. thus constituted are hydathodes.

in the Hedysareae, namely in the genera *Aeschynomene*, *Arachis*, *Chapmannia*, *Cranocarpus*, *Discolobium*, *Geissaspis*, *Herminiera*, *Ormocarpum*, *Smithia*, and *Stylosanthes*. The shaggy hairs of *Smithia* are specially characterized, since the fibrous cells, clothing the shaggy hair, run out into pointed tips, which project like papillae. Lastly, the shaggy hairs of *Cranocarpus Martii*, Benth., which, in correspondence with their shape, will be called anchor-like shaggy hairs ('Ankerzotten,' Fig. 59, *G*), are quite peculiar. In these the anchor-like head, of regular structure and invariably formed by nine cells, is inserted on the longer or shorter, multiseriate stalk, which either becomes slender and only one cell broad towards its upper end, or is broadened out in a club-shaped manner. Of the nine cells composing the head, four, which are arranged in a square, form the chief part of it, whilst their central portion is covered in above by a fifth cell. Between the four cells of the head, four others are intercalated; they are shaped like the flukes of an anchor and are directed downwards. These latter cells have a thickened membrane where they abut on the other cells of the head; elsewhere they have thin walls. Each of them is occupied by a crystal of oxalate of lime, adapted to the shape of the fluke-cell, and inserted in the thickened part of the wall like a tooth in a jaw.

Glandular hairs are not very widely distributed in the Order, but are of various forms. Mention may be made in the first place of small club-shaped external glands composed of few cells and without a distinctly marked stalk, and of others with a distinct stalk and a head of few cells and of varied shape (Fig. 59, *H*). These are fairly widely distributed in the Phaseoleae[1]; they have been found to occur among the Galegeae in *Barbieria*, *Milletia*, *Mundulea*, *Olneya*, *Psoralea* and *Tephrosia*, among the Hedysareae in *Alysicarpus*, *Desmodium*, *Eleiotis*, *Hallia*, *Leptodesmia*, *Lourea* and *Ougeinia*, and among the Dalbergieae in *Hecastophyllum* and *Lonchocarpus*. The glandular hairs of *Pongamia glabra*, Vent. (Fig. 59, *J*) are of special form; here a long cell, forming the head of the gland, but not distinctly marked off, is borne on a long stalk, consisting of 8–12 short cells arranged in a row. The glandular hairs of *Ononis serrata*, Forsk., *O. spinosa*, &c., have a fairly long uniseriate stalk and an ellipsoid head, which is divided by horizontal and vertical walls (Volkens and Behrens); the glands of *Cicer arietinum*, which have long stalks, are similar to these (Martinet).

The peltate glands of *Pterocarpus ancylocalyx*, Benth. (Fig. 59, *K–L*) are essentially different from the forms so far described; the shield of these glands, which is inserted on a group of epidermal cells, is two layers thick, and, when seen in surface-view, shows a group of polygonal cells at its centre, bounded by radially placed ray-cells. Similar peltate or spherical glands also occur in the genera *Brongniartia*, *Glycyrrhiza*, *Harpalyce*, and *Peteria*, belonging to the Galegeae. Different from these peltate glands are those of *Centrolobium robustum*, Mart. and *C. tomentosum*, Benth., in which the shield shows polygonal cells in surface-view, and (this being the most essential feature) encloses an intercellular secretory space within the wall, which is only one cell thick (Fig. 59, *M*). In certain species of *Indigofera* the spherical sessile glandular heads possess a similar intercellular, secretory space. Still another form of gland (Fig. 59, *N*) is very widely distributed among the Phaseoleae in the sub-tribe Cajaneae, and has been met with by Debold in the genera *Atylosia*, *Cajanus*, *Cylista*, *Dunbaria*, *Eriosema*, *Fagelia*, *Flemingia*, and *Rhynchosia*. These glandular hairs are characterized by the considerable size of their approximately spherical heads;

[1] The small club-shaped glands of *Phaseolus multiflorus*, *Vicia sepium* and species of *Psoralea* do not form any oily secretion either in their cell-contents or in their walls, and, regarded physiologically, are water-glands or hydathodes; in some cases and under certain conditions they also secrete carbonate of lime. (For further details see Haberlandt.)

they are inserted on the epidermis by means of a few short basal cells, and are specially peculiar in having the secretion formed in abundance between the cuticle and the cells of the head, which, in the mature gland, are in loose connexion with one another. Lastly, the bulbous hairs (Fig. 59, *O*) are to be included amongst the glandular hairs. They are composed of a few short basal cells and of a spherical or ellipsoid, glandular group of cells; the latter terminates in a simple, tubular, blunt hair, consisting of one or two rows of cells. The structures in question have been observed in species of the genera *Adesmia, Atylosia, Eriosema, Fagelia* (Fig. 59, *O*), *Ormocarpum*, and *Rhynchosia*.

The following types of glands still require to be mentioned: the glandular leaf-teeth of *Myroxylon pubescens* which secrete mucilage and have an epidermis of palisade-like structure (Reinke), the nectar-glands on the stipules or stipels of species of *Vicia, Dolichos, Canavalia, Lablab*, and *Erythrina*, and on the spines of *Erythrina*. The nectar-glands of the species of *Vicia* form spots on the lower side of the stipules and consist of a group of numerous shortly stalked glandular hairs, provided with a 1–4-celled head (Fig. 59, *P–Q*). In *Erythrina crista galli*, L. the nectaries are constituted by the metamorphosed stipels, which enclose a flask-shaped hollow, the base of which is densely clothed with many-celled glandular hairs and conical shaggy hairs (Morini). The spines of *Erythrina* are emergences, at the apex of which a stoma, emitting a secretion, occurs (Delbrouck).

The **petiole** has been investigated by Plitt and Petit in a large number of species. These researches have sufficiently shown that the structure of the petiole is only of importance for the detailed anatomical diagnosis of members of the Family. In the characteristic region the fibrovascular system either forms an arc or a ring of isolated or fused bundles. Either one or two isolated bundles occasionally adjoin the principal annular bundle-system on either side of the groove of the petiole. In many cases the structure of the petiole shows a relation to the herbaceous or woody nature of the plant. Annual herbs, such as *Trifolium*, have an arc of isolated bundles in the characteristic region; herbaceous perennials of higher growth, e. g. *Galega officinalis*, or annual twining plants, like *Phaseolus*, have a ring of isolated bundles; shrubs, such as *Amorpha fruticosa* and *Glycyrrhiza glabra*, have a ring, which is divided into three large segments; trees (*Robinia, Toluifera*) or twining woody plants (*Glycine sinensis*) have a ring of fused or very closely approximated vascular bundles. Differences in the fibrovascular system also occur in the initial region, i.e. in the transverse section through the lowest part of the petiole. Frequently three, but occasionally even five, vascular bundles pass into the petiole, or a ring of bundles is already present in the initial region. Without going further into the details indicated, with regard to which Petit's work in particular should be referred to, it may still be remarked that medullary bundles have not been met with in the petiole in any species; it may be added, however, that, according to C. de Candolle, medullary bundles have been observed in the midrib and rachis of the leaf in *Swartzia tomentosa*.

3. Structure of the Axis. In addition to the older researches of Sanio, Möller, and Solereder, the general structure of the **wood** (i.e. in the woody species) has been especially investigated by Saupe with reference to the Family as a whole, and by Debold, Weyland, Vogelsberger, and Köpff[1] with regard to the tribes investigated by them.

The **vessels** possess a uniform structure in so far as the perforations are simple throughout. In spite of the large number of the genera and species investigated, a scalariform perforation has not been seen in a single case. The size of the lumina of the vessels is very varied. It attains a diameter of

[1] The latter authors have investigated at least one species of each of the genera enumerated above (p. 255) with regard to the structure of the axis (nature of wood and cortex).

·6 mm. in the lianes, e.g. species of *Entada*, while in *Podalyria* the diameter on an average only amounts to ·03 mm. The arrangement of the vessels varies in like manner: isolated vessels occur, for example, in *Amorpha*, groups of vessels in *Carmichaelia*, radial rows of vessels in certain Podalyrieae and Sophoreae. The vessel-wall, where it is in contact with ray- or wood-parenchyma, is usually provided with bordered pits; in many cases, however, the inner slit is indistinct and the pits may probably then be described as simple. Simple pits are found on these parts of the vessel-wall in *Robinia Pseudacacia*, L., large simple pits in *Brya Ebenus*, DC. (Saupe). In many members of the sub-order the bordered pits of the walls of the vessels exhibit the sieve-pit-like structure discovered by Jönsson; as examples of this Jönsson and Heiden enumerate species of *Amorpha, Anthyllis, Apios, Astragalus, Baptisia, Caragana, Clianthus, Colutea, Coronilla, Cyclopia, Cytisus, Dalbergia, Desmodium, Erythrina, Galega, Genista, Glycyrrhiza, Hedysarum, Lathyrus, Lespedeza, Lotus, Lupinus, Medicago, Melilotus, Onobrychis, Ononis, Orobus, Pisum, Psoralea, Robinia, Sophora, Sutherlandia, Swartzia*, and *Thermopsis*. Spiral thickening occurs almost solely in the vessels of narrower lumen and in the tracheides, which are fairly widely distributed in the Family. Such spirally thickened tracheides or vessels of narrow lumen have been found by the different observers in species of *Adenocarpus, Ammodendron, Anthyllis, Calycotome, Carmichaelia, Caragana, Cladrastis, Colutea, Coronilla, Cyclopia, Cytisus* (incl. *Sarothamnus*), *Dorycnium, Edwardsia, Genista, Halimodendron, Lotus, Podalyria, Robinia, Sophora, Spartium, Sweetia, Ulex*, and *Wistaria*. The occurrence of spirally thickened tracheides ('tracheides doliformes') in the secondary medullary rays of *Cytisus Ardoini*, Fourn., and *C. Sauzeanus*, Burn. et Briqu., deserves special notice (Briquet).

The medullary rays are usually narrow, 1–3-seriate. Broad rays, however, also occur; thus Saupe, for example, describes medullary rays 30 cells in breadth in *Sarothamnus scoparius*, 20 cells in breadth in *S. vulgaris*, rays which are 8 cells broad in *Ononis fruticosa*, as much as 6 cells broad in *Anthyllis barba Jovis*, 8 cells in *Carmichaelia*, and so on. The narrow medullary rays are occasionally broadened outwards in the form of a wedge. The medullary rays of some Genisteae (*Adenocarpus, Calycotome, Cytisus, Genista, Spartium, Ulex*) show peculiar knot-like swellings in the neighbourhood of the wood-parenchyma. I will return later to the tier-like arrangement of the medullary rays in some species. According to Saupe, the appearance of the medullary rays in a tangential section may be made use of for the purposes of special classification. In one category the medullary rays consist either of high or of low cells, which are, however, uniform in either case (to be included here are Loteae with high cells: *Anthyllis, Dorycnium, Lotus*; Galegeae with small rounded cells: *Robinia, Sabinea, Wistaria*; with high cells: *Carmichaelia Clianthus, Colutea, Caragana, Halimodendron*; Phaseoleae with large cells: *Dolichos, Erythrina, Hardenbergia, Rhynchosia*; Dalbergieae: *Drepanocarpus, Hecastophyllum, Platymiscium, Pterocarpus*; Sophoreae: *Ammodendron, Cladrastis, Sophora*). In the second case, distinguished by Saupe, the medullary rays are composed of two kinds of cells, both of the high and low form (to be classed here are Podalyrieae: *Brachysema, Jacksonia, Oxylobium, Podalyria, Viminaria*; Genisteae: *Adenocarpus, Argyrolobium, Calycotome, Crotalaria, Cytisus, Genista, Goodia, Hovea, Spartium*, and *Ulex*; Galegeae: *Amorpha, Indigofera, Psoralea*; Hedysareae: *Arthrocarpum, Brya, Coronilla, Desmodium, Lespedeza*; Sophoreae: *Virgilia*).

In most cases the wood-prosenchyma forms the groundwork of the wood and is characterized by its simple pits[1]. Xylem, in which the whole

[1] Even in *Inocarpus* (*Bocoa provacensis*, Aubl.) and *Pterocarpus* according to Strasburger (loc. cit.) and contrary to a statement of Höhnel's (Sitz.-Ber. Wiener Akad., 1884, loc. cit.) with reference to this point.

prosenchymatous groundwork of the wood is provided with bordered pits, and is thus differentiated like tracheides, does not occur in any of the Papilionaceae, nor indeed in any of the Leguminosae. Differences occur with regard to the thickness of the wall and the size of the lumen. Very frequently the walls of the prosenchymatous elements are characterized by the possession of an inner gelatinous membrane. Saupe met with gelatinous cross-bars, which traverse the lumina of the prosenchymatous elements in species of *Clianthus*, *Lespedeza*, *Psoralea* and *Sabinea*. Starch-containing prosenchyma-cells are, according to Saupe, present in *Sabinea*, *Robinia* and *Sophora*, septate prosenchyma-cells in species of *Sabinea* and *Sophora*. Lastly, reference may be made to the peculiar 'corroded' nature of the walls of the prosenchyma-cells in *Swartzia Martii*, Eichl. and *S. cardiosperma*, Spruce (see Köpff), a peculiarity which has also been repeatedly observed in species of other Orders.

The wood-parenchyma is often abundantly developed; it frequently forms tangential bands, which enclose the vessels. As an example, we may mention the red sandal-wood. In many cases chambered parenchyma containing crystals is also developed.

To complete our account of the structure of the wood the following series of features may be referred to: the peculiar appearance of the transverse section of the wood, observed in certain Genisteae and also in genera of other tribes, the tier-like construction of some Papilionaceous woods, the structure of the wood of some Papilionaceous lianes, the structure of the light, spongy wood of *Herminiera* and some other genera, and lastly, the coloured woods occurring in the Sub-order.

Saupe has described a peculiar appearance in the transverse section of the wood of some Genisteae (*Adenocarpus*, *Calycotome*, *Cytisus*, *Genista*, *Spartium*, *Ulex*): starting from the ring of spring-wood, which is rich in vessels, bands, made up of narrow vessels, spiral tracheides and wood-parenchyma, traverse the remaining portion of the secondary wood in an oblique direction, so that the entire transverse section presents a net-like pattern; he also met with similar features in *Ononis*, in *Anthyllis*, *Dorycnium*, and *Lotus*, in *Caragana*, and *Halimodendron*, in *Coronilla*, and *Edwardsia*.

The tier-like construction of the wood, which, however, also occurs in other Orders, has been observed by Höhnel in a relatively small number of species (*Andira anthelminthica*, Benth., *Bocoa provacensis*, Aubl., species of *Dalbergia* pro parte, *Dipteryx odorata*, Willd., *Myrocarpus* sp., and species of *Pterocarpus*), to which Saupe adds *Arthrocarpum*, *Hecastophyllum*, and *Platymiscium*. The tier-like structure of the wood is chiefly due to the fact that the medullary rays are of equal height and are arranged in a tier-like manner. This peculiar arrangement can occasionally even be recognized by the naked eye, e.g. in a very well marked manner in red sandal-wood, a tangentially split surface of which appears striated by delicate horizontal lines. In certain woods the tier-like structure extends to the tracheides and libriform; in this case it can be recognized in longitudinal sections, especially by the fact that special areas (Tüpfelfelder), rich in pits, occur near the ends of and at an equal height on the walls of the cells concerned, thus forming continuous tiers. The tier-like structure is naturally only present in relatively thick pieces of the axis. From a systematic point of view one gathers from Höhnel's statements that, although this feature is so characteristic, it could not always be demonstrated in the same species.

With regard to the above-mentioned structure of the wood in some Papilionaceous lianes, namely in *Mucuna* sp. and *Dioclea* sp. according to H. Schenck, in *Pueraria Thunbergiana*, Benth. according to Avetta, and in *Phaseolus Caracalla*, L. according to Borzi, it may be mentioned that the wood-parenchyma is thin-walled and unlignified, especially in the later-formed secondary wood. In the lianes of the Papilionaceae, as in those of other Orders, axial wood of denser structure occurs in the neighbourhood of the pith.

The light woods also deserve special mention; they form the floating apparatus of stems which vegetate on the surface of the water, and occur in some species belonging to the genera *Aeschynomene*, *Erythrina*, *Geissaspis*, *Herminiera*,

and *Soemmeringia* (cf. Fig. 60). The structure of *Herminiera Elaphroxylon*, Guill. et Perr. (*Aedemone mirabilis*, Kotschy) is best known and will therefore be described first. The wood of this plant has no annual rings. Its groundwork is formed by cells with wide lumina and thin walls, showing an arrangement in radial rows in transverse section, and tier-like arrangement in longitudinal section, and having the

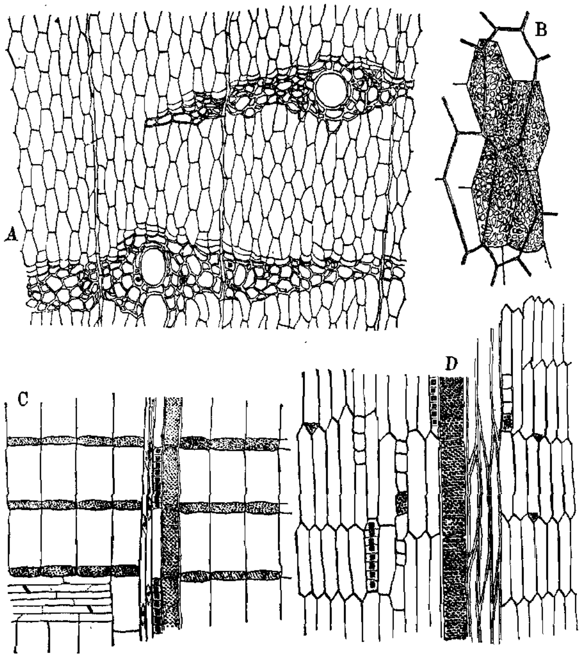

FIG. 60. Wood of *Aeschynomene*, sp. A, Transverse section through the wood; B, Part of a transverse section, showing the terminal surfaces of the transversely-cut fibrous cells, which have wide lumina; C, Radial longitudinal section; D, Tangential section (compare the description of the analogous structure of the wood of *Herminiera* in the text).—Original.

form of hexagonal prisms with their end-surfaces inclined at about 45° to the radial plane. The end-walls have a sieve-like structure, being traversed by numerous pores; on the longitudinal walls of the cells either no pits or only a few are found. The contents of the cells, so far as examined, consist of air [1]. This loose xylem-tissue is

[1] Möller's statement regarding *Aeschynomene aspera*, Willd. is not quite in agreement with this. According to him delicate spiked crystals ('feine spiessige Krystalle'), which he figures, occur in the prismatic cells of this plant.

traversed by tangential bands of wood-fibres, which have thicker walls and the usual small cross-section, and enclose a single vessel or a small group. At the boundaries of these transverse bands transitional forms between the prismatic and fibrous cells occur, and also crystal-containing chambered fibres, which were erroneously interpreted by E. Hallier. The medullary rays are generally narrow, and 1- or 2-seriate; their cells are elongated in the radial direction, and bear extraordinarily abundant pits on the walls with which the successive cells of a radial row touch one another. In older pieces of the wood of *Herminiera Elaphroxylon*, besides the narrow medullary rays, broader rays occur; the latter include a vascular strand which consists of spiral vessels, sheathed by pitted vessels with wider lumina, and runs for a variable distance towards the pith. Klebahn has proved that these vascular elements in the broad medullary rays correspond to the vascular part of the rudiment of a root, which is formed in the cortex of *Herminiera*, between each of the broad medullary rays and a lenticel corresponding to the latter on the surface of the stem. According to Vogelsberger, the characteristic structure of the wood of *Herminiera Elaphroxylon* is scarcely evident in young branches (herbarium-material), because the prismatic cells only occur in subordinate amount in them. According to Möller, *Erythrina crista galli*, L. exhibits the same structure in the wood as *Herminiera*; except that here the vessels lie in a ground-tissue, formed of prismatic cells, and not in bands of wood-fibres. Among the species of *Aeschynomene*, which, however, do not all have the wood-structure of the ambatsch-plant, some agree with *Herminiera* as regards the arrangement of the vessels, others with *Erythrina*. According to Hallier, Möller, and Vogelsberger, the following species show the structure under discussion: *Aeschynomene americana*, L., *A. aspera*, L., *A. brasiliana*, DC., *A. falcata*, DC., *A. hispida*, Willd., *A. hispidula*, H. B. K., and *A. indica*, L., likewise *A. Sellowi*, Vog., and *A. sulcata*, H. B. K., although less typically, but not *A. dimidiata*, Welw.; according to Vogelsberger, *Geissaspis cristata*, W. et A., *G. tenella*, Benth., and *Soemmeringia semperflorens*, Mart.[1] also show it.

Lastly, with regard to the coloured woods (species of *Baphia*, *Pterocarpus*, &c.), we may add that the colouring matter chiefly impregnates the walls of the woody tissue.

The structure of the **cortex** is well known through the researches of Möller, Debold, Weyland, Vogelsberger and Köpff. The development of the cork varies; it has been investigated by Sanio, J. E. Weiss and Douliot, as well as by the authors mentioned above. The cork arises either in the epidermis, or subepidermally, or in one of the superficial cell-layers of the primary cortex, or in the middle of it, or in the innermost layer of the primary cortex, or in some cases on the inner side of the primary groups of hard bast. It is noteworthy that occasionally in one and the same species the place of origin of the cork may vary between the second and the sixth cell-layer of the primary cortex, an irregularity which hitherto has not been found to be so marked in any other Order. According to Möller the cork-cells mostly have thin walls, while moderately flattened in form (*Caragana*, *Colutea*, *Robinia*, *Sophora*), or have uniformly thickened walls (*Amorpha*, *Andira*), or walls sclerosed on one side (*Geoffroya*, *Virgilia*), or transitions from this latter type to a sclerosed condition on all sides (*Cytisus*). In a species of *Adesmia* described by Güssfeld (Reise in den Anden von Chile und Argentinien) as 'flammende Wachs-Papilionacee' but not further designated, the cork-cells are filled with a resinous substance (Volkens).

The following genera have epidermal development of cork: amongst the Galegeae *Coursetia*, *Indigofera* pro parte, *Mundulea* and *Robinia*, according to Weyland; among the Hedysareae *Pseudarthria*, *Pycnospora* and *Uraria*, according to Vogelsberger; among the Sophoreae *Myroxylon* and *Virgilia*, and among the Genisteae *Sarothamnus* and *Ulex*, according to Douliot. The cork arises subepidermally or in the second to sixth cell-layer, sometimes at a variable depth in the

[1] The walls of the cells in the light woods in question only give slight wood-reactions (with phloroglucin and hydrochloric acid, as also with aniline salts). The walls consist of lignocellulose (for details regarding this see Hancock and Dahl, Lignocellulose, Ber. d. deutsch. chem. Gesellsch., Bd. xxviii, p. 12).

same species; among the Phaseoleae in *Calopogonium*, *Canavalia*, *Centrosema*, *Cratylia*, *Phaseolus*, *Pueraria*; among the Galegeae in *Amorpha*, *Calophaca*, *Dalea*, *Diphysa*, *Eysenhardtia*, *Indigofera* pro parte, *Robinia*, *Sabinea*; among the Hedysareae in *Aeschynomene*, *Coronilla*, *Cranocarpus*, *Desmodium*, *Geissaspis*, *Hallia*, *Herminiera*, *Leptodesmia*, *Lespedeza*, *Nissolia*, *Onobrychis*, *Ormocarpum*, *Ougeinia*, *Pictetia*, *Smithia*, *Soemmeringia*, *Stylosanthes*; among the Dalbergieae in *Centrolobium*, *Dalbergia*, *Geoffroya* and *Pterocarpus*; among the Genisteae in *Cytisus*; among the Sophoreae in *Sophora* and of the Swartzieae in *Calycandra*. The cork arises in the middle of the primary cortex: among the Phaseoleae in *Atylosia*, *Camptosema*, *Cleobulia*, *Clitoria*, *Cologania*, *Cylista*, *Eriosema*, *Erythrina*, *Galactia*, *Rhynchosia*, *Rudolphia*; among the Galegeae in *Indigofera denudata*, Thunb. and *Psoralea*; and among the Sophoreae in *Dalhousiea*. The cork is formed in the innermost layer of cells of the primary cortical parenchyma in species of *Cicer*, *Dioclea*, *Galega*, *Glycine*, *Lotus*, and *Trifolium*. In species of *Hippocrepis*, *Lathyrus*, *Medicago*, *Onobrychis*, *Ononis* and *Orobus*, Douliot has found the place of origin of the cork to vary, lying either in the endodermis or in a cell-layer in the middle of the primary cortex. Lastly, pericyclic cork is developed on the inner side of the primary groups of bast-fibres in *Adesmia*, *Colutea*, *Cytisus*, *Halimodendron*, *Sphaerophysa* and *Soja*[1].

Formation of aerenchyma in place of the cork has only been observed in a few cases (*Sesbania marginata*, Benth. and *Lotus uliginosus*, Schk., according to Schenck; *Sesbania aculeata*, Pers., according to Scott; and *Phaseolus* in water-cultures, according to Perseke).

With regard to the structure of the primary cortex, it may be noted that this tissue is often collenchymatous in its outer portion and frequently contains groups of stone-cells. In many woody species, principally in plants with reduced leaves ('blattarme Pflanzen'), of which there are a large number in the sub-order, especially among the Podalyrieae, Genisteae, and Galegeae, a considerable part of the primary cortex is developed as palisade-parenchyma or as assimilatory tissue of some other form. Associated with this feature we find: (*a*) an abundant occurrence of stomata in the epidermis of the stem, and, in species with grooved stems, restricted to the grooves; and (*b*) frequently also the occurrence of strands of sclerenchyma-fibres, which either run in the primary cortex independently or in connexion with the fibro-vascular system, or traverse the cortex; for further details see Pick, Volkens, Schube, Ross, Briquet, Diels, Reiche, Pasquale and Reinke. Likewise, with regard to the structure of the wings of the stem ('macroptères' of Briquet), which are found in certain Podalyrieae, Genisteae, and Vicieae, and to some extent form a continuation of the primary cortex, reference must be made to the literature.

As examples, the stem-structure of *Cytisus Ardoini*, Fourn. (Fig. 61, *A*) and of *C. Sauzeanus*, Burn. et Briqu. (Fig. 61, *B*) will now be described according to Briquet's account, his diagrammatic figures of the transverse section being reproduced. A transverse section of the stem of *Cytisus Ardoini* shows eight grooves cut across, by which the stem is longitudinally furrowed, and, between these, eight longitudinal ridges, which are T-shaped in transverse section ('microptères' of Briquet). The epidermis of the longitudinal ridges has a thick external wall and bears no stomata and no hairs. Below it a hypoderm with thin walls occurs; then follows a plate of sclerenchyma-fibres, which stretches beneath the whole of the epidermis of each ridge, and the middle of which projects inwards in the form of a slight ridge. The epidermis of the grooves, on the other hand, has a delicate external wall, includes stomata and bears hairs. In the grooves abundant assimilatory tissue is situated subepidermally. Opposite both the grooves and the ridges the innermost part of the primary cortex up to the pericycle is formed by colourless tissue composed of large cells with thin walls. The stem of *C. Sauzeanus*, a species which is very nearly

[1] To ensure a correct understanding of the statements made above, it should be remarked that the mode of development of the cork is in general not constant for the genus. A detailed enumeration of the species, in which the one or the other mode of cork-development has been observed, is only omitted so as to economize space.

related and also very similar to *C. Ardoini*, has quite a different structure. It is only 5-angled and is not deeply grooved. In this species the epidermis of the stem is of approximately uniform nature at all points of the transverse section. At each angle hypodermal tissue lies below the epidermis, followed by a column of sclerenchyma-fibres, which has a T-shaped cross-section and extends as far as the pericycle; while at the five lateral surfaces abundant assimilatory tissue is developed below the epidermis, and the innermost part of the primary cortex is occupied by colourless tissue. These two examples sufficiently show that the structural features in question may be successfully employed for the distinction of species, as has been done by Briquet (loc. cit.) for the species of *Cytisus*.

In very many cases the outer limit of the bast is formed by isolated groups of hard bast; in the neighbourhood of these groups or between them stone-cells

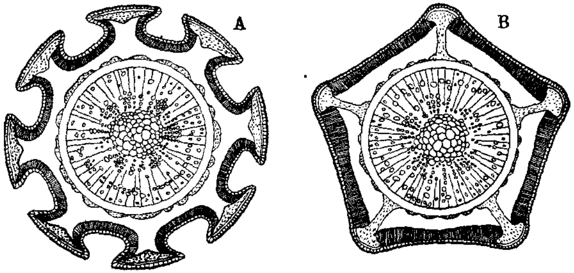

FIG. 61. Diagrammatic figures of the transverse section of young shoots of *Cytisus Ardoini*, Fourn., and B *Cytisus Sauzeanus*, Burn. et Briqu. (In both drawings the epidermis is shown; the colourless hypoderm and the similarly constituted tissue of the primary cortex are left blank; the green tissue is shaded; the elements of the hard bast are represented by dotting.)—After Briquet.

or groups of crystal-cells may occur in places. In the same region in other species, a ring of bast-fibres is stated to occur; this ring, however, probably only exists in the young branch, and subsequently either becomes broken up into isolated groups of bast-fibres or is converted into a composite and continuous sclerenchymatous ring. The latter has likewise been demonstrated in a number of the members of the sub-order.

The following genera possess isolated groups of bast-fibres in the pericycle: among the Galegeae, *Astragalus*, *Brongniartia*, *Carmichaelia*, *Caragana*, *Corynella*, *Coursetia*, *Dalea* (with the exception of *D. polyadenia*, Torr., in which crystal-cells replace the bast-fibres; with regard to this see above, p. 267), *Diphysa*, *Eysenhardtia*, *Halimodendron*, *Indigofera*, *Lessertia*, *Mundulea*, *Petalostemon*, *Psoralea*, *Sabinea*, *Sphaerophysa*, *Tephrosia*; all the Hedysareae investigated by Vogelsberger (see above) with the exception of *Desmodium* and *Ougeinia*; among the Dalbergieae, *Dalbergia*, *Drepanocarpus*, *Euchresta*, *Geoffroya*, *Hecastophyllum*, *Machaerium*, *Platymiscium*, *Platypodium*, *Poecilanthe*, *Pterocarpus*, *Tipuana*; lastly, among the Sophoreae, *Ammodendron*, *Calpurnia*, *Cladrastis*, and *Sophora*. A ring of bast-fibres occurs in the pericycle in *Colutea* pro parte, *Galega*, *Glycyrrhiza*, and *Harpalyce* according to Weyland, and in *Desmodium* pro parte according to Vogelsberger. A composite and continuous sclerenchymatous ring is developed: among the Galegeae in *Amorpha*, *Barbieria*, *Calophaca*, *Colutea* pro parte, *Milletia*, *Olneya*, *Robinia* and *Wistaria*; quite generally in the Phaseoleae, according to Debold; in *Ougeinia*, among the Hedysareae; in *Andira*, *Centrolobium*, *Derris*, *Dipteryx*, *Lonchocarpus*, *Muellera*, *Piscidia*, *Pongamia*, *Pterodon*, among the Dalbergieae; in *Bowdichia*, *Dalhousiea*, *Diplotropis*, *Myrospermum*, *Myroxylon*, *Ormosia*, *Sweetia* and *Virgilia*, among the Sophoreae; in *Aldina*, *Swartzia* and *Zollernia*, among the Swartzieae.

The secondary bast frequently contains secondary groups of bast-fibres, which are compact, do not border directly on the medullary rays, and in many cases cause a stratification of the bast. The secondary as also the primary bast-fibres are occasionally, like the wood-fibres, furnished with a gelatinous layer. Crystal-containing chambered fibres with ordinary rhombohedra or styloid-like crystals in the loculi are the usual elements accompanying the bast-fibres. According to Möller, short articulations and the exclusive occurrence of simple sieve-plates are characteristic of the sieve-tubes. In the sieve-tubes of *Robinia Pseudacacia* and of *Wistaria sinensis*, Strasburger has recently observed peculiar mucilage-bodies, which frequently have an angular shape and are connected with the sieve-plates by means of fine threads; following Strasburger Baccarini has demonstrated these bodies in a large number of genera belonging to the different tribes. The medullary rays of the bast are mostly fairly broad, more than four cells in breadth, never sclerosed, and considerably broadened towards the exterior.

The statements regarding the structure of the axis made up to this point relate chiefly to woody plants. The stems of the herbaceous species have been investigated by Jännicke, especially in relation to the arrangement of the vascular bundles and the nature of the interfascicular tissue.

Jännicke distinguishes a series of types, of which the following may be mentioned. The first occurs in most species of *Trifolium*, and consists in the vascular bundles being united by interfascicular tissue, composed of parenchymatous sclerenchyma, which is connected externally with the groups of hard bast belonging to the vascular bundles. Interfascicular tissue composed of parenchymatous sclerenchyma and situated within the cambium characterizes species of *Coronilla*, *Ornithopus*, *Scorpiurus* and *Securigera*, and likewise *Onobrychis sativa*, in which small intermediate bundles also occur; interfascicular tissue in the same position, but consisting of sclerenchymatous prosenchyma and parenchyma, is found in species of *Astragalus*, *Astrolobium*, *Biserrula*, *Coronilla*, *Galega*, *Hippocrepis*, *Lotus*, *Medicago*, *Melilotus*, *Ononis*, *Phaca*, *Tetragonolobus* and *Trigonella*. Lastly, in *Dorycnium*, according to Jännicke, the interfascicular tissue situated within the cambium consists solely of sclerenchyma-fibres.

To conclude the description of the structure of the axis the occurrence of cortical vascular bundles and the remaining anomalous structural features of certain species, lianes or otherwise, may be considered. **Cortical vascular bundles** are probably universally present in those species which possess winged stems, e.g. *Genista sagittalis* or *Bossiaea scolopendria*, but frequently also in those species which are provided with grooved stems, some of these being forms with reduced leaves. The latter case occurs in the following species: *Retama Raetam*, Webb et Berth., *Genista pilosa* and *G. tinctoria* (according to Russell), *Cytisus linifolius*, L. and *C. monspessulanus*, L. (according to Briquet). The cortical vascular bundles are of greater systematic significance in the Vicieae, where they have been met with in all investigated species of the genera *Vicia*, *Ervum*, *Lathyrus*, *Orobus* and *Pisum*, in two opposite angles of the stem, either singly or several together, one behind the other.

The remaining **anomalies** of the Papilionaceous lianes and non-lianes in those cases which have been determined with certainty, consist either (*a*) in the appearance of successive rings of growth in the pericycle or in the primary cortex, rarely in the bast (in species of *Wistaria*, *Mucuna*, *Spatholobus*, *Pueraria*, *Pachyrhizus*, *Rhynchosia*, *Dalbergia*, and *Machaerium*[1]), or (*b*) in the formation

[1] The concentric stratification of the wood met with in older shoots of *Astragalus* (*A. macropus*, Bunge, according to my own observation) does not depend on the occurrence of successive rings of growth, but is due to the fact that the xylem-mass is interrupted by rings of unlignified parenchymatous tissue, which has thin walls and contains spiral tracheae, the inner part still showing the cambial radial arrangement of its cells. Quite analogous structures occur, as may be recalled here, among the Cruciferae in the genus *Vella* and among the Caryophylleae in the

of groups of phloem in the tissue of the wood (in species of *Mucuna*, *Dioclea*, and *Phaseolus*). Secondary cleavage of the mass of wood has not been observed. The stems of Papilionaceous lianes are mostly cylindrical; species of *Machaerium* and *Rhynchosia phaseoloides* have band-shaped stems.

The following statements may be made regarding the detailed structure of the anomalous Papilionaceous stems. Among the Galegeae successive rings of growth are only present in *Wistaria chinensis*, DC., in which they have been investigated by De Bary, Crüger, Leclerc du Salbon, Licopoli, Strasburger, and others. The anomaly first appears in axes 2.5 cm. thick, and Licopoli also met with it in the root. The secondary zones of wood and bast originate in the primary cortex on the outer side of the pericyclic composite and continuous sclerenchyma-ring. In the Vicieae no anomalous stem-structure occurs apart from the cortical vascular bundles, which have already been discussed above. The anomalous stem described by Wakker as *Abrus precatorius*, L., according to Schenck belongs to *Rhynchosia phaseoloides* (see below); *Abrus precatorius* itself has normal structure. Among the Phaseoleae, the tribe which presents the largest number of cases of anomalous stem-structure, a stem, described by H. Schenck as *Mucuna* sp., and probably belonging to *M. altissima*, DC., unites the anomaly of successive rings of growth with the occurrence of phloem-islands in the wood. In *Mucuna* the formation of the secondary rings of growth takes place late and in the pericyclic parenchyma. The islands of soft bast are embedded in the outer xylem-tissue of the vascular ring, which is rich in unlignified parenchyma, and are given off from the cambium on its inner side. According to H. Schenck, another species of the same genus, *Mucuna pruriens*, DC., only exhibits the successive rings of growth, which Fritz Müller was the first to demonstrate in *Mucuna*. In possessing islands of soft bast, *Phaseolus Caracalla*, L. agrees with *Mucuna*, according to Borzi, and here, as in the latter plant, unlignified portions of tissue with thin walls occur in the older wood. This unlignified tissue and likewise the medullary rays of the wood and bast contain small bundles of sieve-tubes, which are formed secondarily from the thin-walled tissue. H. Schenck has observed a similar structure in a stem 2.4 cm. thick, belonging to a species of *Dioclea*. The remaining Phaseoleae with anomalous structure have only successive rings of growth. Firstly, as regards the genus *Spatholobus*, Gamble's statements indicate that *Spatholobus Roxburghii*, Benth. shows this anomaly. Conclusive proof of this has been brought forward by Debold, who also demonstrated that the secondary rings of growth in *S. Roxburghii* arise extrafascicularly on the outer side of the composite and continuous sclerenchyma-ring of the cortex. According to Debold, a second species of the same genus, *Spathylobus littoralis*, Hassk. (Zollinger, No. 86, Herb. Zürich), shows the same anomaly; but here the anomalous growth takes place on the inner side of the composite and continuous sclerenchyma-ring, that is to say, in the pericycle. The successive rings of growth of *Pueraria Thunbergiana*, Benth., which Avetta observed in stem and root, as in *Mucuna*, arise in the pericyclic parenchyma, and the same applies to those of *Pachyrhizus montanus*, DC., according to Chodat; and lastly, those found in the band-shaped stems of *Rhynchosia phaseoloides*, DC.[1] (Crüger, Wakker) and of *R. reticulata* (Saupe), arise in the primary cortical parenchyma on the outer side of the sclerenchyma-ring. In connexion with these anomalous Phaseoleae it may be remarked that other lianes belonging to the Phaseoleae, e.g. *Canavalia gladiata*, 'Benth.,' according to H. Schenck, and *Hardenbergia monophylla* according to Saupe, are normal in structure. Among the Dalbergieae, successive rings of growth occur, according to Gamble, in the arborescent species, *Dalbergia paniculata*, Roxb.; on the other hand, according to H. Schenck, *Dalbergia variabilis*, Vog., *D. Muelleri*, Taub., *D. foliolosa*, Benth., have normal structure, and also, according to Gamble, *D. Sissoo*, Roxb., *D. latifolia*, Roxb., *D. cultrata*, Grah., *D. lanceolaria*, L., *D. nigrescens*, Kurz, *D. stipulacea*, Roxb., and *D. foliacea*, Wall., of which *D. stipulacea* alone belongs to the lianes. In the genus *Machaerium* also a certain number only of the species possess the anomaly in question. Thus *Machaerium brasiliense*, Vog., and *M. violaceum*, Vog., are normal in structure according to H. Schenck; whereas the following are anomalous: *M. aculeatum*,

genus *Acanthophyllum*. When the thin-walled tissue dries up, as is the case in herbarium-material, the mass of wood can without difficulty be separated into several concentric cylinders in this plant, as in the other cases.

[1] According to Wakker the anomaly in question also occurs in the root of *R. phaseoloides*.

Raddi, *M. amplum*, Benth., *M. angustifolium*, Vog., *M. secundiflorum*, Mart., and *M. tounateifolium*, Taub. In these latter the appearance of the transverse section varies; the stem is usually round, but in *M. aculeatum* it is winged. The secondary rings of growth generally arise in the phloem-parenchyma of the original ring of bundles. Lastly, a stem, labelled *Derris* sp. by H. Schenck, and possibly belonging to *D. negrensis*, Benth., also possesses secondary strands of wood and bast.

Before leaving these stems with anomalous structure two further anomalous stems may be taken into consideration, which have previously been discussed in the literature, and which, to judge by their detailed anatomical structure, almost certainly belong to the Papilionaceae. These are stem No. 495 of Schenck's collection of woods, and Martius's stem No. 254[1], which is mentioned by Radlkofer. This stem of Schenck's, which he has represented in his Fig. 119 on Plate IX, shows strands of wood and bast of various sizes in the secondary cortex. The anomalous structure only appears at a late stage; the oldest bundles of wood and bast occur at the outside and are the largest; the inner ones are smaller and arise later. A transverse section of the stem in some measure recalls that of *Serjania piscatoria*, Radlk. The second piece

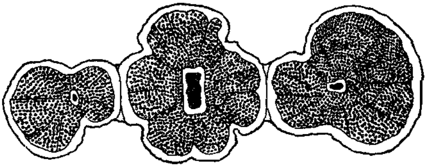

FIG. 62. A piece of the stem of one of the Papilionaceae (undetermined) with compound xylem-mass. Natural size.—Original.

(that of Martius, cf. Fig. 62) has a compound xylem-mass and at the first glance gives the impression of being composed of three stems fused together.

4. STRUCTURE OF THE ROOT. On this subject see Lohrer (1887, loc. cit.). The roots with anomalous structure have already been mentioned above in the description of the anomalous stem-structures. With regard to their anatomical structure, it need only be mentioned that, according to Van Tieghem (Ann. sc. nat., sér. 5, t. xiii, 1871, p. 217), primary hard bast is of frequent occurrence in the roots of the Papilionaceae, as also of the Caesalpinieae and Mimoseae, and that a sub-epidermal supporting network ('réseau de soutien') is described by Russow (Betracht. Leitb. und Grundgew., 1875, p. 73) in a species of *Hedysarum*.

II. CAESALPINIEAE.

1. REVIEW OF THE ANATOMICAL FEATURES. Only a few anatomical features are common to the whole of the Caesalpinieae, namely simple perforations in the vessels, wood-prosenchyma with simple pits, superficial development of cork, and a composite and continuous sclerenchymatous ring at the outer margin of the bast. As compared with the other Leguminosae, it is especially noteworthy that oxalate of lime, besides occurring in the form of solitary crystals, frequently appears in the form of clustered crystals, and that simple unicellular hairs are very widely distributed; the tannin-sacs of the

[1] Exactly similar pieces of stem, perhaps from the same source, have also been found in the collections at Kew, at Paris, and recently also at Munich. The figure given above was made from the piece at Munich.

Papilionaceae are, as a rule, absent [1] or are only rudimentary in their development, and do not appear as idioblasts.

As regards the other anatomical features of the Caesalpinieae, reference may be made to the following points. The type of stoma is not uniform; the stomata may or may not be accompanied by subsidiary cells, placed parallel to the pore. Internal secretory organs are not uncommonly developed, viz. in the form of secretory cells (species of *Caesalpinia, Cassia, Diptychandra, Mezoneurum, Pterolobium, Wagatea*), schizogenous secretory cavities (in *Caesalpinia* pro parte, *Cenostigma, Copaifera, Eperua, Hymenaea, Peltogyne, Prioria,* and *Trachylobium*), and secretory canals (in the axis of *Eperua* and *Copaifera*). The hairy covering consists of clothing and glandular hairs of varied structure. Special forms of clothing hairs are: unicellular hooked hairs (*Apuleia, Dialium, Labichea*), unicellular two-armed hairs (*Moldenhawera*), two-celled malpighian hairs (*Bauhinia confertiflora*, Benth.), bristle-like shaggy hairs (*Cassia*), stellate or tufted trichomes (*Cassia*), hairs branched like a fir-tree (*Cenostigma*), shaggy hairs with a spherical and glandular multicellular base (*Cassia*, Fig. 63, *A, B*). The glandular hairs also possess very varied structure. Special types of glandular hairs are the boat-shaped, shortly stalked, glandular hairs, enclosing an intercellular secretory space, found in species of *Bauhinia* (Fig. 63, *C*), and the depressed glandular hairs of species of *Berlinia, Dicorynia, Heterostemon,* and *Humboldtia* (Fig. 63, *D*). True anomalous stem-structure only occurs in certain species of *Bauhinia*, and consists either in the appearance of successive zones of wood and bast or, on the other hand, in the splitting up of the xylem-mass (Fig. 64, *C*).

Finally, a series of anatomical features, which may be made use of in specific and occasionally even in generic diagnosis, remains to be mentioned. Among these are: the rare formation of hypoderm in the leaf, the frequent papillose differentiation of the lower epidermis of the leaf, gelatinization of the epidermis of the leaf, occurrence of solitary or of clustered crystals in the epidermis of the leaf (species of *Apuleia, Copaifera, Eperua,* and *Saraca*), occurrence of cells with mucilaginous walls (species of *Berlinia, Cassia, Cercidium, Macrolobium,* and *Peltogyne*), of sclerenchyma-fibres (species of *Heterostemon, Saraca,* and *Schotia*), and of peculiar sclerenchymatous cells, containing silica in their lumina (*Cynometra*) in the mesophyll, the varied structure of the veins of the leaf (whether vertically transcurrent or embedded, &c.), development of abundant wood-parenchyma in the form of tangential bands in the wood, occurrence of secondary bands of hard bast, and so on.

2. STRUCTURE OF THE LEAF. The leaf-structure has been thoroughly investigated by Dellien [2]. The results of this investigation form the basis of the following statements.

The **epidermis** of the leaf is mostly one-layered. Development of hypoderm is rare. In *Dicorynia paraensis*, Benth. (but not in *D. floribunda*, Spruce, which is regarded as a form of this species), in *Cassia incurvata*, Benth., and *C. Blancheti*, Benth., hypoderm occurs on both sides of the leaf; in *Ceratonia Siliqua*, L., *Cercidium texanum*, A. Gray, and *Parkinsonia aculeata*, L., only above the lower epidermis. Other differences in the structure of the epidermis consist in the

[1] Dellien affirms their entire absence; but Trécul notes their occurrence in *Ceratonia* in the pith and in the cortex, in the latter on the inner side of the primary hard bast.

[2] Dellien investigated numerous species of the following genera, which are enumerated according to Bentham and Hooker's arrangement: *Sclerolobium, Diptychandra, Poeppigia, Campsiandra, Cenostigma; Peltophorum, Mezoneurum, Caesalpinia, Hoffmanseggia, Haematoxylon, Pterolobium, Gymnocladus, Gleditschia, Wagatea, Poinciana, Schizolobium, Moldenhawera, Cercidium, Parkinsonia; Dicorynia, Cassia, Labichea, Apuleia, Dialium, Ceratonia; Bauhinia, Cercis; Brownea, Heterostemon, Amherstia, Humboldtia, Macrolobium, Berlinia, Eperua, Afzelia, Tamarindus, Schotia, Tachigalia, Peltogyne, Hymenaea, Trachylobium, Saraca, Crudia; Copaifera, Prioria; Hardwickia, Pterogyne, Cynometra; Dimorphandra.*

special shape of the cells or special structure of the cell-walls. The epidermal cells of species of *Sclerolobium*, e.g. *S. paniculatum*, Vog., are elongated like palisade-cells. *Caesalpinia sepiaria*, Roxb., *C. Hildebrandtii*, Baill., *C. laxa*, Benth., *Cynometra racemosa*, Benth., *Cassia Chamaecrista*, L., *C. glandulosa*, L., and *C. Tora*, L., as well as *Pterolobium lacerans*, R. Br., have a subpapillose epidermis. Distinct formation of papillae has been observed in the following species: *Apuleia praecox*, Mart.; *Bauhinia confertiflora*, Benth.; *Caesalpinia Nuga*, Ait.; *Cassia acosmifolia*, Mart., *C. alata*, L., *C. fastuosa*, Willd., *C. moschata*, H.B.K., *C. obtecta*, Benth., *C. scabra*, H.B.K., *C. viscosa*, Pohl; *Crudia pubescens*, Spruce; *Dialium guineense*, Willd., *D. platysepalum*, Bak.; *Dicorynia floribunda*, Spruce; *Dimorphandra mollis*, Benth., *D. parviflora*, Spruce; *Hardwickia binata*, Roxb.; *Labichea punctata*, Benth.; *Macrolobium acaciaefolium*, Benth., *M. multijugum*, Benth.; *Peltophorum dasyrhachis*, Kurz; *Schizolobium excelsum*, Vog.; *Wagatea spicata*, Dalz. The papillae of *Macrolobium acaciaefolium* have a peculiarly lobed outline, and in surface-view almost hide the contours of the epidermal cells; the papillae of *Cassia obtecta* and *C. scabra* are long and finger-shaped and sclerosed. In *Bauhinia confertiflora* the formation of papillae is combined with the occurrence of a many-layered epidermis; the epidermis becomes many-layered by division and the uppermost layer of cells is provided with peculiar lobed papillae. The outer walls of the epidermal cells are only rarely (*Hymenaea, Trachylobium*) strongly thickened. In *Cassia secunda*, Benth., and *C. hypoleuca*, Mart., the epidermal cells acquire an appearance like that of stone-cells in surface-view, owing to a peculiar manner of thickening of the cell-walls. Gelatinization of the epidermal cells, which is valuable for characterizing species, is not very widely distributed. According to Walliczek it occurs in the plants which form the source of senna-leaves; according to Dellien also in numerous other species of *Cassia*, and in *Caesalpinia ferrea*, Mart. var., *C. Hildebrandtii*, Baill., *C. laxa*, Benth., *C. microphylla*, Mart., *C. mimosoides*, Lam.; *Crudia amazonica*, Spruce; *Cercis chinensis*, Bunge, *C. Siliquastrum*, L.; *Cercidium texanum*, A. Gray; *Dialium divaricatum*, Vahl; *Dimorphandra exaltata*, Schott, *D. Gardneriana*, Tul., *D. parviflora*, Spruce; *Haematoxylon Campechianum*, L.; *Hoffmanseggia falcaria*, Cav., *H. stricta*, Benth.; *Peltophorum dasyrachis*, Kurz, *P. Vogelianum*, Benth.; *Poinciana elata*, L., *P. regia*, Boj. Solitary crystals and more rarely clustered crystals of oxalate of lime occur as special constituents of the contents of the epidermis. The solitary crystals, which have been observed in *Saraca indica*, L., and species of *Copaifera* (*C. coriacea*, Mart., *C. elliptica*, Mart., *C. guianensis*, Desf., *C. Langsdorfii*, Desf., *C. Martii*, Hayne, *C. oblongifolia*, Hayne, *C. officinalis*, L., *C. rigida*, Benth., and *C. trapezifolia*, Hayne, but not in *C. confertiflora*, Benth., and *C. multijuga*, Hayne), are contained singly in smaller epidermal cells, or in pairs of these, or, lastly, in the chambers of epidermal cells divided by several septa. *Apuleia praecox*, Mart. has smaller epidermal cells with clustered crystals; *Eperua rubiginosa*, Miq., contains small clustered crystals singly in the cells of its epidermis, 2–5 such cells being grouped together; lastly, *Saraca triandra*, Bak., has clustered and solitary crystals. In *Ceratonia Siliqua*, L., peculiar contents are found in epidermis and hypoderm; they consist of pale brown tannin-containing masses, which are lamellated so as to appear striated, insoluble in water, alcohol, ether, chloroform, and potash solution, and soluble in *Eau de Javelle*.

In most of the Caesalpinieae the **stomata** are present only on the lower surface of the leaf. Numerous stomata are found on the upper side of the leaf, especially in many species of *Cassia*, and besides these in species of some few other genera, *e.g. Caesalpinia* and *Cercidium*. As a rule, the guard-cells are in the same plane as the epidermal cells; occasionally, however, they are depressed below the level of the epidermis, and in rare cases (*Ceratonia Siliqua*, L., *Bauhinia*

confertiflora, Benth., and *Caesalpinia Nuga*, Ait.) this even amounts to the formation of a vestibule above the stoma. As regards the detailed structure of the guard-cells, a noteworthy feature is the frequent occurrence on the outer wall of a thickening-ridge, like the flap of an envelope in shape. The Caesalpinieae vary in regard to the occurrence of subsidiary cells. A certain number of the genera possess subsidiary cells, which are placed parallel to the pore, while in the other genera subsidiary cells are absent, and the stomata are surrounded by three or more epidermal cells. These features are occasionally not even constant for a given species, inasmuch as stomata, with several irregularly orientated neighbouring cells, may occur on the same leaf side by side with stomata which have parallel subsidiary cells. This must be taken into consideration in making use of the following statements.

According to Dellien the following plants have parallel subsidiary cells: *Afzelia, Amherstia, Apuleia, Berlinia, Brownea, Caesalpinia* pro parte, *Campsiandra, Cassia, Cenostigma, Copaifera, Crudia, Cynometra, Dialium, Dicorynia, Dimorphandra* pro parte, *Diptychandra, Eperua, Haematoxylon, Hardwickia, Heterostemon, Hoffmannseggia, Humboldtia, Hymenaea, Macrolobium, Mezoneurum, Moldenhawera, Peltogyne, Peltophorum dasyrachis*, Kurz, *Poinciana, Prioria, Pterolobium, Saraca, Schizolobium, Schotia latifolia*, Jacq., *Sclerolobium, Tachygalia, Tamarindus, Trachylobium*, and *Wagatea*; while the following have stomata without special subsidiary cells: *Caesalpinia* pro parte, *Ceratonia, Cercidium, Cercis, Dimorphandra* pro parte, *Gleditschia, Gymnocladus, Labichea, Parkinsonia, Peltophorum Vogelianum*, Benth., *Poeppigia, Pterogyne, Schotia speciosa*, Jacq. var. *tamarindifolia*, Harv.

The **mesophyll** is in most cases (a few species excepted, especially those belonging to the genera *Hoffmanseggia* and *Hymenaea*) bifacial in structure. Special features of the mesophyll, apart from the secretory organs, which will be treated separately, are as follows: occurrence of stone-cells in the mesophyll of *Macrolobium chrysostachyum*, Benth. (stone-cells here in the epidermis also), in the spongy tissue of *Saraca indica*, L., and *S. triandra*, Bak., and in the parenchyma of the veins in *Moldenhawera cuprea*, Pohl, as well as the occurrence of sclerenchyma-fibres in the mesophyll in *Saraca indica*, L., *S. triandra*, Bak., *Heterostemon ellipticus*, Mart., and *Schotia speciosa*, Jacq., var. *tamarindifolia*, Harv., and of peculiar sclerenchyma-cells, to be described in detail immediately, in all the investigated species of *Cynometra*. The last-named elements were first observed by Radlkofer in *C. cauliflora*, L., in which they give rise to transparent dots, which are either directly visible or only after the leaf has been cut across. The sclerenchyma-cells which are present here abut on the vascular bundles by means of their bulbously-enlarged bases; their outer branched ends resemble fibres and extend below the epidermis, especially on the upper side of the leaf, while the enlarged basal portion is occupied by a clear glistening mass, which is occasionally transversely split, and consists of silica. Besides sclerenchymatous cells of this kind, others independent of the veins now and then occur; these extend below the epidermis on both sides of the leaf and are likewise filled with silica; further, in certain species of the same genus there are sclerenchyma-cells, which unite the upper and lower epidermis like girders. In connexion with this peculiar deposition of silica the occurrence of silicified groups of cells in the palisade-tissue of *Apuleia praecox*, Mart., may be mentioned; these cells cause transparent dots in the leaf.

The vascular bundles of the **veins** of the leaf are mostly provided with sclerenchyma, and, in veins of medium size, are embedded or vertically transcurrent.

Dellien describes embedded veins in *Afzelia, Berlinia, Caesalpinia, Cassia, Cercidium, Cercis* pro parte, *Crudia, Cynometra, Dialium* pro parte, *Dimorphandra* pro parte, *Gleditschia, Gymnocladus, Haematoxylon, Heterostemon, Hoffmanseggia, Macrolobium, Mezoneurum, Moldenhawera, Parkinsonia, Peltyogyne, Peltophorum Vogelianum*, Benth., *Poeppigia, Poinciana, Prioria, Pterogyne, Pterolobium, Saraca, Schizolobium, Schotia*, and *Tamarindus*; vertically transcurrent veins in *Amherstia*,

Apuleia, Brownea, Campsiandra, Cenostigma, Cercis pro parte, *Copaifera, Dialium* pro parte, *Dicorynia, Dimorphandra* pro parte, *Diptychandra, Eperua, Hardwickia, Humboldtia, Hymenaea, Labichea, Peltophorum dasyrachis,* Kurz, *Sclerolobium, Tachigalia, Trachylobium,* and *Wagatea.*

Oxalate of lime is deposited in the form of solitary and clustered crystals according to the statements both of Borodin and Dellien. While clustered crystals scarcely occur at all in the Papilionaceae, and in the Mimoseae are restricted to two or three genera, their occurrence is a common phenomenon in the Caesalpinieae. The solitary crystals are especially found accompanying the veins; the clustered crystals chiefly free in the mesophyll. As in the two other sub-orders of the Leguminosae, solitary crystals occasionally also occur in the palisade-tissue, enclosed in local thickenings of the cell-wall; e. g. in *Eperua leucantha,* Benth., *E. rubiginosa,* Miq., *Macrolobium latifolium,* Vog., *Tachigalia paniculata,* Aubl., and *Tamarindus indica,* L. The occurrence of crystals in the epidermis of the leaf has already been discussed above.

Internal **secretory organs** of varied nature are of widespread occurrence. Secretory cells with various contents, mucilaginous cells, secretory cavities and secretory canals are found, while tannin-sacs, so widely distributed in the Papilionaceae, are, according to Dellien and Baccarini, only of a rudimentary type or do not occur at all.

The secretory cells frequently cause pellucid dots in the leaf, and are of ellipsoid shape in the palisade-tissue, while those in the spongy parenchyma usually have a spherical form. In *Cassia Blancheti,* Benth., they are situated in the palisade-tissue directly below the upper epidermis of the leaf and possess brown tanniniferous contents and mucilaginous walls. In *Diptychandra* (*D. aurantiaca,* Tul., and *D. glabra,* Benth.) secretory cells filled with pale yellow contents, which are soluble in alcohol, occur in the mesophyll; *Wagatea spicata,* Dalz., possesses similar elements. The secretory cells of the following plants may be classed with those just mentioned: species of *Caesalpinia* belonging to the sections *Nugaria* (*C. Nuga,* Ait.), *Guilandina* (*C. Bonducella,* Flem., *C. Bonduc,* Roxb., *C. echinata,* Lam.), *Sappania* (*C. Sappan,* L., *C. sepiaria,* Roxb., *C. pulcherrima,* Sw., *C. pauciflora,* Benth. et Hook., *C. Hildebrandtii,* Baill.) and *Coulteria* (*C. tinctoria,* Domb.), also *Caesalpinia bahamensis,* Lam., *C. Crista,* L., and *C. Grahami,* Hort. Calcutt. inedit., *Mezoneurum cucullatum,* W. et A., and *Pterolobium lacerans,* R. Br. Dellien met with mucilaginous cells in the mesophyll in *Berlinia acuminata,* Soland.; *Cassia Galeottiana,* Martens; *Cercidium texanum,* A. Gray; *Macrolobium acaciaefolium,* Benth., *M. chrysostachyum,* Benth., *M. guianense,* Aubl., *M. latifolium,* Vog., *M. multijugum,* Benth., *M. pendulum,* Willd.; *Peltogyne densiflora,* Spruce. These mucilaginous cells usually occur immediately below the epidermis on either side. Like the secretory cells, secretory cavities are also fairly widely distributed. They are throughout of schizogenous origin (not lysigenous, as Taubert erroneously states), and in correspondence with this fact are lined by a distinct epithelium. In the case to be first considered, they contain a yellow resin soluble in alcohol, and cause transparent dotting of the leaves; e. g. in the genera *Copaifera, Eperua, Hymenaea, Peltogyne, Prioria,* and *Trachylobium.* In *Cenostigma* (*C. Gardnerianum,* Tul., with its var. *latifolium,* Benth., and *C. macrophyllum,* Tul.) and the following species of *Caesalpinia* of the section *Caesalpinaria* (*C. bracteosa,* Tul., *C. laxiflora,* Tul., *C. microphylla,* Mart., and *C. pyramidalis,* Tul.) the contents of the secretory cavities are of a different nature, being brown in colour and including tannin, and consequently producing opaque dots in the leaf. In *Copaifera,* according to Rhein, Tschirch, and Guignard, the secretory cavities are partially replaced in the axis by secretory canals. While the primary cortex of the branch of *Copaifera* contains a ring of short oil-cavities, and oil-cavities elongated like canals occur in the pith, schizogenous secretory canals (schizolysigenous, according to Sieck; compare Rhein's statements quoted below) appear in the secondary wood (but not in the secondary cortex); these canals anastomose with one another, and only occur in the spring-wood; it is interesting that, according to Guignard, the epithelial cells of these interxylary resin-canals are directly formed by transformation of cambial cells. According to Rhein, however, side by side with these secretory canals, produced, so to speak, from the cambium, others arise subsequently in the mature tissue of the wood, by the schizogenous

origin of a small intercellular space, which subsequently becomes enlarged in a lysigenous manner. Finally, secretory canals also occur in the wood and primary cortex of *Eperua falcata*, Aubl. (Mezger); as to the origin of the interxylary secretory canals of *Eperua* it is only known that they become secondarily enlarged in a lysigenous manner.

The varied **hairy covering,** consisting of clothing and glandular hairs, remains to be discussed. The characteristic uniseriate hairs of the Papilionaceae with one or a few short basal cells and a long terminal cell have not been observed in the Caesalpinieae; on the other hand, simple unicellular hairs of varied shape and length are common. Special forms of these unicellular hairs are the following: the thin-walled, superficially granulated hairs of *Cassia armata*, Wats., which are shaped like a pruning-hook; the short hairs of *Cassia occidentalis*, L., which have a wide lumen and are curved like a horn; the spear-shaped hairs of *Dialium platysepalum*, Bak., both longitudinal sides of which are provided with one or two tooth-like prongs towards the end of the hair; the bracket-hairs or hooked hairs in species of the genera *Apuleia*, *Dialium*, and *Labichea*; lastly, the two-armed hairs of *Moldenhawera*. Two-armed hairs, bicellular owing to their being provided with a stalk-cell, have been observed in a species of *Bauhinia* (*B. confertiflora*, Benth.). Of the trichomes with more complicated structure, mention may first be made of the long bristle-like shaggy hairs, which consist of several rows of cells and have been observed in *Cassia secunda*, Benth., and *C. obtecta*, Benth. In other species of the same genus (*Cassia aurivilla*, Mart., *C. fuscescens*, Benth., *C. villosa*, Mill.) hairs of a stellate or tufted nature occur. These consist of an emergence of variable size, at the apex of which more or less numerous, simple, unicellular hairs are inserted in a stellate or tufted manner. Trichomes, branched like a fir-tree, occur in *Cenostigma*; they are formed by an emergence, resembling a stem, in which numerous simple uniseriate hairs are sunk, and stand out like branches.

With the hairs of *Cassia secunda*, &c., referred to above, other shaggy hairs having a glandular function must be classed; the base of these hairs is spherically swollen and is composed of numerous polyhedral cells. The filiform end of the hair, attached to this spherical basal portion, consists of a few rows of cells and forms either the apical (*Cassia trachycarpa*, Vog., Fig. 63, *A*) or the lateral (*Cassia cathartica*, Mart.) continuation of the glandular basal part. Glandular hairs of this kind were met with by Dellien in a considerable number of species of *Cassia*. In the glandular shaggy hairs of some other species of *Cassia* (*C. aurivilla*, Mart., Fig. 63, *B*, *C. fuscescens*, Benth., and *C. setosa*, Vog.) a peculiar phenomenon occurs, as the epidermal cells of the glandular base are in part produced into simple unicellular hairs. Lastly, in *Cassia geminata*, Benth., the glandular shaggy hairs are placed on filiform multiseriate emergences, the superficial cells of which are likewise in part elongated into unicellular hairs.

The remaining external glands, occurring in the Caesalpinieae, may be subdivided into the following types. Large club-shaped glands, visible even to the naked eye and consisting of numerous polygonal cells, are found on the margin of the leaf in the Gleditschieae and in *Cassia occidentalis*, L., and in the former are supported at their base by simple unicellular hairs. Glands, which correspond in structure with the glandular basal portion of the shaggy hairs described above, have been observed in *Cassia incurvata*, Benth., *Pomaria glandulosa*, Cav. (=*Caesalpinia bijuga*, Sw.; in this case sunk in emergences of the leaf-margin) and in some species of *Caesalpinia*, belonging to the section *Caesalpinaria* (e. g. *C. bracteosa*, Tul.); in these last they have a distinct multiseriate stalk of variable length. A further type of gland is represented by the shortly stalked boat-shaped glands of many species of *Bauhinia* (Fig. 63, *C*), which exhibit an intercellular secretory space within a one-layered sheath, the cells of which are polygonal in surface-view. A special form of gland occurs in *Cassia*

neglecta, Vog., namely, one shaped like a fiddle with a smaller, approximately spherical basal portion and a larger terminal part, both parts being composed of polygonal cells. The following glands are collectively distinguished from those so far described by their small size. They may be subdivided into stalked and sessile forms ; the latter only project slightly above the surface of the organ and may therefore also be described as depressed glands. The stalked glands, better described as those that project above the surface of the organ, include the club-shaped few-celled glandular hairs of *Dialium*, *Sclerolobium*, and *Tachigalia*, as well as those with a unicellular stalk and a head, which is unicellular or may be two-celled owing to the presence of a vertical wall (*Apuleia praecox*, Mart.). The depressed glandular hairs include the multicellular retort-shaped hairs of *Berlinia angolensis*, Welw., and *Humboldtia Baillonii*, Schweinf. (Fig. 63, *D*), which have a spherical, multicellular and glandular basal part, penetrating deep into the mesophyll, and a short neck-portion, which only projects a little above the surface of the leaf, and is formed by a laterally directed, hair-like, terminal cell ; to this type also belong the trichomes of *Berlinia acuminata*, Soland.,

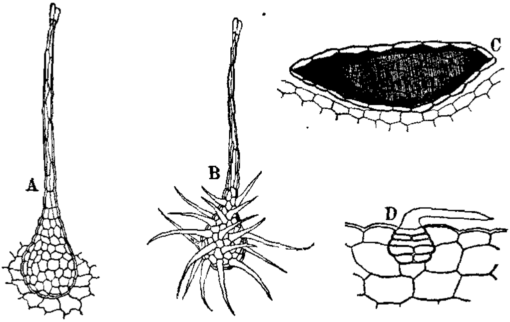

FIG. 63. Special forms of hairs of certain *Caesalpinieae*. A, Glandular shaggy hair of *Cassia trachycarpa*, Vog. ; B, Glandular shaggy hair of *Cassia aurivilla*, Mart. ; C, Boat-shaped gland with intercellular secretory space of *Bauhinia Bongardi*, Steud. ; D, External gland of the leaf of *Humboldtia Baillonii*, Schweinf.—Original.

Dicorynia paraënsis, Benth. and *Heterostemon mimosoides*, Desf., which are quite similarly constituted. Finally, mention may be made of (*a*) the glandular structures, which produce the black dotting of the lower side of the leaf in *Caesalpinia Gilliesii*, Wall. ; the epidermis, which is somewhat arched outwards at this point, and the polygonal secretory cells lying below it, are concerned in the formation of these glands ; (*b*) the large and very variously shaped nectarial glands on the leaves of many species of *Cassia*, the secretory tissue having no typical palisade-like epithelium in *Cassia Canca*, Cav. (according to Morini) ; and (*c*) the pearl-glands, observed by Meyen on the stem of *Bauhinia anatomica*, which agree in their structure with the well-known pearl-glands of the Cecropieae.

The structure of the **petiole** has hitherto only been investigated in some species of *Bauhinia*, *Caesalpinia*, *Cassia*, *Ceratonia*, *Cercis*, *Copaifera*, and *Tamarindus* by Petit. The course and arrangement of the fibro-vascular system vary. In some cases the same types of transverse section as in the arborescent Papilionaceae are found in the characteristic region ; but in other cases (*Bauhinia*, *Cercis*) more complicated conditions occur. A few facts only need be noted here with respect to

the two genera last named. In *Bauhinia racemosa* the fibro-vascular system at the base of the petiole exhibits three rings of wood and bast; in its further course through the petiole this vascular system repeatedly shows an arrangement in two concentric rings, the inner of which is inversely orientated as regards the position of wood and bast; lastly, in the characteristic region the vascular system consists of four arcs of wood and bast, which are arranged in a line at right angles to the line of symmetry of the petiole, the two central arcs of bundles having their bast-portions turned towards one another, while the two outer arcs have their bast-portions directed outwards. In *Cercis Siliquastrum* the fibro-vascular system begins with three isolated vascular bundles, which subsequently fuse to form a ring, while near the characteristic region the fibro-vascular system consists of five rings of wood and bast, and lastly, in the characteristic region itself of three rings, of which the middle one is open towards the upper side.

3. STRUCTURE OF THE AXIS. The structure of the **wood** has been investigated especially by Möller, Solereder, and Saupe. The vessels have lumina of varied size, which is often considerable in the lianes, and have exclusively simple perforations. Sieve-like structure of the bordered pits of the vessels has been observed by me in species of *Amherstia*, *Cassia*, and *Cynometra*. According to Saupe, tracheides occasionally occur in the Caesalpinieae (species of *Gymnocladus*, *Gleditschia*, and *Cercis*), and, like the pitted vessels with narrower lumina, are spirally thickened. The medullary rays are mostly narrow, especially in herbarium-branches. But in older stems of species of *Haematoxylon*, *Gymnocladus*, *Gleditschia*, and *Caulotretus*, medullary rays five to eight cells in breadth are mentioned by Saupe. In the cases investigated by him, the cells of the medullary rays are of uniform nature, being small and rounded in tangential section. A tier-like arrangement of the medullary rays has been observed in species of *Cassia*, *Caesalpinia*, *Cercis* and *Caulotretus* (Höhnel and Saupe). Wood-parenchyma is not uncommonly developed in abundance, frequently in the form of tangential bands; e. g. according to Möller, in species of *Haematoxylon*, *Caesalpinia* pro parte, *Dicorynia*, *Eperua*, *Bauhinia*, *Detarium* and *Gleditschia*, and, according to Saupe, also in species of *Brownea*, *Cassia* pro parte, *Cercis* and *Hymenaea*. Crystal-containing parenchyma has been observed in species of *Bauhinia* and *Cercis*. The wood-prosenchyma, as in the rest of the Leguminosae, has simple pits throughout. Transverse beams of a gelatinous nature have been observed in the wood-prosenchyma of species of *Bauhinia* (Saupe); a gelatinous layer of the cell-wall likewise occurs, for example, in *Bauhinia*. In the coloured woods (*Caesalpinia echinata*, Lam. and *Haematoxylon campechianum*, L.) the colouring matter is chiefly stored in the walls of the wood-prosenchyma. Septation of the wood-prosenchyma by thin cross-walls is, according to De Bary, found in *Ceratonia Siliqua*, and, according to Saupe, in species of *Bauhinia*. According to Saupe, fibrous cells, which store up starch, occur in species of *Cassia*, *Caesalpinia* (*Guilandina*), *Bauhinia*, *Ceratonia*, *Hymenaea* and *Brownea*.

The structure of the **cortex** has been investigated by Möller in species of *Gleditschia*, *Gymnocladus*, *Caesalpinia*, *Tamarindus*, *Cassia*, *Bauhinia* and *Ceratonia*. Dellien also makes some noteworthy statements on this subject. According to Möller, the cork arises subepidermally in *Gymnocladus canadensis*, Lam., *Tamarindus indica*, L., *Cassia auriculata*, L., *Bauhinia aculeata*, Vell., *Ceratonia Siliqua*, L., and in the second or third cell-layer of the primary cortex in *Gleditschia monosperma*, Walt. The cork-cells are strongly flattened in *Gleditschia* and *Tamarindus*, less so in *Bauhinia* and *Gymnocladus*, cubic in *Cassia* and *Ceratonia*. They have thin walls in *Gleditschia* and *Bauhinia*, and somewhat thicker ones in *Gymnocladus*; the walls are uniformly sclerosed on all sides in *Cassia*, thickened on one side in *Ceratonia* (on the inner tangential wall) and in *Tamarindus* (on the outer tangential wall). In almost all the genera and species investigated by Dellien, a composite and continuous scleren-

chymatous ring is present at the outer limit of the bast. *Bauhinia forficata*, Link (*B. aculeata*, Vell.) alone forms an exception to this, while in other *Bauhinias* the composite and continuous sclerenchymatous ring is present. The outer part of the primary cortex is occasionally differentiated as collenchyma. Stone-cells also occur in the primary cortex (species of *Gleditschia, Gymnocladus*). Solitary crystals are chiefly found in connexion with the sclerenchymatous ring. Hard bast is not uncommonly developed in the secondary bast, and is occasionally stratified. Solidly constructed plates of bast-fibres, which are widely distributed in the Papilionaceae, are, however, absent here. In *Caesalpinia echinata*, Lam. the bands of bast-fibres are replaced by groups of stone-cells. Solitary crystals are of frequent occurrence in the bast; side by side with them clustered crystals are occasionally present. The sieve-tubes are shortly articulated, and have scalariform sieve-plates. According to Baccarini the sieve-cells of *Cassia* and *Poinciana* contain the mucilage-bodies discovered by Strasburger; they are more widely distributed in the Papilionaceae, where they were described in detail[1]. The medullary rays of the bast are frequently broadened towards the exterior and never become sclerotic between the groups of bast-fibres.

Anomalous stem-structures are not very frequent and are essentially restricted to the stems of certain species of *Bauhinia*. Apart from these, some species of *Cassia* possess grooved stems[2], viz. *Cassia quinquangulata*, Rich., according to Crüger, and *C. angulata*, Vog., according to H. Schenck. Among the *Bauhinias*, some of the species are characterized by normal structure of the axis. Some of these have band-shaped or winged and undulated stems (Fig. 64, *A–B*). According to H. Schenck, *Bauhinia Blumenaviana*, H. Schenck is referable to this type, and, according to the same author, the piece of stem, described by Warburg under the name *Caulotretus heterophyllus*, belongs to the same species of *Bauhinia*. The band-shaped stems of this species are produced during the growth in thickness of the young branches, owing to the cambium being confined to two opposite sides—the ultimate narrow sides—of the stem, while on the broad sides, in the median line of which the leaves and branches are inserted, little secondary growth in thickness takes place. Otherwise the growth is completely normal, as has already been mentioned. Formation of wings and ribs on the broad sides is also occasionally found in the older stems. As regards the anatomy of these band-shaped but otherwise normally constructed stems, we may add that there is a ring of dense wood around the pith, which is of cruciate shape in all the *Bauhinias*[3], while the periaxial wood, present in the wings, is of looser structure and is characterized by the presence of vessels with wide lumina, and thin-walled, unlignified wood-parenchyma. In some other species of *Bauhinia* successive formation of new zones of growth has been observed, e.g. according to H. Schenck, in *B. rubiginosa*, Bong. and *B. angulosa*, Vog., and, according to Brandis and Gamble, in *B. Vahlii*, W. et A. In the two species first mentioned the secondary formation has been shown to take place in the pericyclic parenchyma on the inner side of the sclerenchymatous ring. In the older stems of *B. angulosa* subsequent dilatation takes place in the outer part of the wood, and it is not improbable that fission of the mass of wood may set in in still older stems. A third group

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[1] Baccarini's statement that the mucilage-bodies are not contained in the sieve-tubes of the Caesalpineae is incorrect, and is to be attributed to the fact that Baccarini appears not to be aware that *Cassia* and *Poinciana* are not members of the Papilionaceae but of the former sub-order.

[2] The young branches of the species concerned are not grooved.

[3] According to Hérail young branches of *Bauhinia speciosa* have a four-lobed cross-section corresponding to the cruciate cross-section of the pith, around which the wood, bast and primary cortex are uniformly developed. Subsequently the wood becomes rounded off in consequence of growth in thickness, and the branch becomes cylindrical.

of *Bauhinias* shows fission of the xylem-mass of the stem (Fig. 64, *C*). Of the representatives of this type, the only one determined with certainty is *B.*

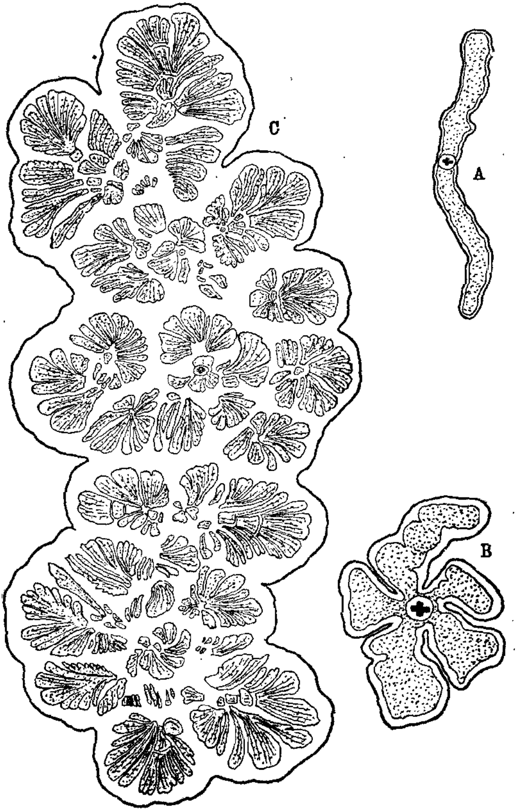

FIG. 64. A, Winged and undulated stem of *Bauhinia*, sp. (H. Schenck, collection of woods, no. 167) B *Bauhinia rubiginosa*, Bong. C, Split xylem-mass of *Bauhinia Langsdorffiana*, Bong. A and B, natural size C, approximately natural size.—After H. Schenck.

Langsdorffiana, Bong., collected by H. Schenck. In this species the fission o the wood commences with the dilatation of the thin-walled wood-parenchyma

the segments of wood, thus separated, become surrounded by a cambium, which produces wood internally and bast externally; they subsequently undergo further fission. During this breaking up of the wood the central mass of xylem either remains unaffected or may also become divided up. According to Warburg (and contrary to Crüger's statements) fission of the wood in the *Bauhinias* occurs not only in the stem but also in the root.

NOTE.—With regard to the structure of the root, Van Tieghem mentions the occurrence of a supporting network ('réseau de soutien') in the main roots of species of *Cassia* (*C. floribunda*, *C. florida*, and *C. polyantha*). A layer of cells in the primary cortex, situated immediately outside the endodermis, is characterized by the fact that the middle portion of the radial and transverse walls of the cells have lignified ridge-like thickenings, which meet at the corners and correspond in neighbouring cells, and in this manner form a tangentially placed network with rectangular meshes.

III. MIMOSEAE.

1. REVIEW OF THE ANATOMICAL FEATURES. The few anatomical characters which distinguish all members of the Mimoseae are such as either belong to the other Leguminosae also, or are at least present in a certain number of the Papilionaceae and Caesalpinieae. Of these the following may be mentioned: the type of stoma, which is accompanied by subsidiary cells, placed parallel to the pore; the universal presence of variously shaped glandular hairs; the superficial development of cork; the composite and continuous sclerenchyma-ring in the pericycle; the simple perforations of the vessels; and the wood-prosenchyma with simple pits. Oxalate of lime is mostly present in the form of solitary crystals, which either exhibit the ordinary rhombohedral form or a styloid-like shape, and are occasionally embedded in thickenings of the cell-wall; clustered crystals have only been observed within the genera *Mimosa* and *Piptadenia*. The internal secretory system is much less developed than in the Papilionaceae and Caesalpinieae. Sacs with wide lumina and various contents are common in the soft bast; they correspond to the well-known tannin-sacs of the Papilionaceae; further, in certain species of *Calliandra*, *Pentaclethra*, *Pithecolobium* and *Prosopis*, secretory cells occur, and in species of *Pithecolobium*, secretory cavities surrounded by bracket-cells. The hairy covering consists of simple and compound clothing hairs and of glandular hairs. The simple clothing hairs are unicellular or uniseriate; special forms are: one-armed hairs (*Xylia*, *Inga*) and unicellular hooked hairs (*Calliandra*). The compound clothing hairs (see Fig. 65, *A–C*) are represented by variously constituted shaggy (*Mimosa*) and tufted hairs (*Pentaclethra*, *Prosopis*). In like manner the glandular hairs, which are universally distributed, exhibit various forms; in these hairs the head, apart from the details of its structure, may be ellipsoid, spherical or peltate; peculiar branched glandular hairs have also been observed (*Mimosa Spruceana*, Benth., Fig. 65, *D–E*). Beyond the occurrence of medullary vascular bundles with concentric structure in *Elephantorhiza Burchellii*, Benth. and of furrowed stems in some species of *Acacia* and *Piptadenia*, anomalous stem-structure is found only in the genus *Entada*, in which bundles of sieve-tubes arise—probably by subsequent divisions—in the secondary wood. It remains to be mentioned that numerous anatomical characters, especially those presented by the leaf-structure, are of value for more special diagnosis. Among these we may include: papillose differentiation of the epidermis of the leaf (in species of *Albizzia*, *Calliandra*, *Enterolobium*, *Mimosa*, *Pithecolobium*, *Stryphnodendron*); gelatinization of the epidermis of the leaf (in species of almost all the genera, see below); division of the

epidermal cells of the leaf by means of delicate vertical walls (*Albizzia*, *Enterolobium*); occurrence of crystals in the epidermis of the leaf (*Parkia filicoidea*, Welw.); silicification of cells of the epidermis or mesophyll (in species of *Calliandra* and *Pithecolobium*); differentiation of a middle layer in the mesophyll; occurrence of sclerenchyma-fibres in the leaf-tissue (in species of *Affonsea*, *Calliandra*, *Inga*, *Parkia*, *Pithecolobium*, *Prosopis*, *Schrankia* and *Stryphnodendron*); and lastly the varied structure of the trichomes.

2. STRUCTURE OF THE LEAF. The leaf-structure has been investigated especially by Coester[1], whose observations are shortly reproduced in the following description.

With regard to the **integumental tissue** it is noteworthy that hypoderm has not been found in any member of the Mimoseae. The outline of the epidermal cells in surface-view varies. Subpapillose differentiation of the epidermal cells, especially of those on the lower side of the leaf, is not uncommon; it is described by Coester in the case of species of *Entada*, *Plathymenia*, *Piptadenia*, *Stryphnodendron*, *Gagnebina*, *Elephantorhiza*, *Prosopis*, *Leucaena*, *Adenanthera*, *Lysiloma*, *Calliandra*, *Serianthes*, *Albizzia*, *Pithecolobium*, and *Enterolobium*. In other species typical papillae are formed, but exclusively on the lower side of the leaf. In this case the papillae are either short and hemispherical (*Stryphnodendron polyphyllum*, Mart., *S. floribundum*, Benth.; *Calliandra lanata*, Benth., *C. scutellifera*, Benth.; *Pithecolobium corymbosum*, Benth., *P. microcarpum*, Benth., *P. parvifolium*, Benth., *P. Saman*, Benth.; *Mimosa obovata*, Benth.; *Enterolobium ellipticum*, Benth., and *E. Timbouva*, Mart.), or mammiform, owing to the middle portion of the outer wall alone protruding (*Mimosa Spruceana*, Benth.; *Albizzia ferruginea*, Benth., *A. pallida*, Fourn.; *Pithecolobium marginatum*, Benth., *P. montanum*, Benth., *P. polycephalum*, Benth.; *Enterolobium Schomburgkii*, Benth.), or finger-shaped (*Pithecolobium Clypearia*, Benth., *P. trapezifolium*, Benth.; *Albizzia procera*, Benth.). The cuticle is occasionally smooth, but in most cases it is covered with verrucose or granular irregularities. Now and then deposits resembling wax give the leaves a whitish appearance, e.g. in *Acacia cultriformis*, A. Cunn., or *Mimosa rigida*, Benth. A different condition of the leaf-surface, in which it appears coated with varnish, is caused either by resinous excretion from glandular hairs (*Acacia dodonaeifolia*, Willd.) or by the structure of the cuticle itself (in *Mimosa calodendron*, Mart., *M. calothamnus*, Mart. and others). The outer walls of the epidermal cells are in many cases (species of Acaciae Phyllodinae, *Calliandra* and *Mimosa*) considerably thickened. In some species of *Acacia* and *Mimosa* these outer walls form ridge-like external projections, either on the whole surface of the leaf or only in the neighbourhood of the stomata. The inner walls of the epidermal cells are only rarely (*Calliandra*) strongly thickened; gelatinization of the inner walls, on the other hand, is of more frequent occurrence, and has been observed in species of *Parkia*, *Entada*, *Stryphnodendron*, *Piptadenia*, *Elephantorhiza*, *Adenanthera*, *Dichrostachys*, *Neptunia*, *Schrankia*, *Leucaena*, *Desmanthus*, *Mimosa*, *Acacia*, *Lysiloma*, *Serianthes*, *Calliandra*, *Albizzia* and *Pithecolobium*. Occasionally (*Mimosa*, *Acacia*) a few cellulose-lamellae are still retained in the mucilaginous membranes. Secondary division of the epidermal cells by delicate vertical walls is not common. It is of very regular occurrence in *Enterolobium*, where the cells are often divided into from 4 to 8 chambers; in *Albizzia ferruginea*, Benth., in addition to the vertical divisions, others occur, which are parallel to the surface of the leaf, and in this

[1] Coester's investigations extend to numerous species of the following genera: 1. Parkieae: *Pentaclethra*, *Parkia*; 2. Piptadenieae: *Entada*, *Plathymenia*, *Piptadenia*; 3. Adenanthereae: *Xylia*, *Stryphnodendron*, *Adenanthera*, *Elephantorhiza*, *Gagnebina*, *Prosopis*, *Dichrostachys*, *Neptunia*; 4. Eumimoseae: *Desmanthus*, *Mimosa*, *Schrankia*, *Leucaena*; 5. Acacieae: *Acacia*; 6. Ingeae: *Lysiloma*, *Calliandra*, *Albizzia*, *Pithecolobium*, *Enterolobium*, *Serianthes*, *Inga* and *Affonsea*.

species the papillae have similar division-walls. Special contents of the epidermal cells, viz. crystals of oxalate of lime, have been observed in *Parkia filicoidea*, Welw., where they have a columnar shape. Silicification of epidermal cells and of subjacent cells of the palisade-tissue occurs in species of *Calliandra* and *Pithecolobium*.

The **stomata** are often restricted to the lower side of the leaf; e.g. in the Parkieae, Ingeae and some of the Adenanthereae, isolated occurrence of stomata above the veins being disregarded. On the other hand, the Eumimoseae, the Acacieae and the genera *Neptunia* and *Dichrostachys* belonging to the Adenanthereae, have uniform distribution of the stomata on both sides of the leaf. To some extent this distribution of the stomata stands in relation to the size of the pinnules. The large leaflets of the Ingeae have stomata on the lower surface only: the narrow and small leaflets of the Mimoseae have them on both sides. In the narrow pinnules and phyllodes the stomata are frequently arranged parallel to one another and to the midrib. Coester observed a peculiar disposition of the stomata in *Piptadenia peregrina*, Benth., *P. macrocarpa*, Benth., *Mimosa rhodostachya*, Benth., *M. somnians*, Humb. et Bonpl., and *M. trijuga*, Benth. In these plants the stomata on the lower side of the leaf are found crowded together at the bases of the leaflets, whilst those on the upper side are present in large numbers at the tips of the leaflets, the remaining parts of the lower and upper side respectively being free from stomata. This peculiar disposition of the stomata may possibly be connected with the manner in which the leaflets cover one another in the sleep-position. In *Mimosa cruenta*, Benth., at any rate, this has been shown to be the case. In this species the stomata occur on the whole of the upper surface, but only on one longitudinal half of the lower side of the leaflets; the lowest leaflet has no stomata at all on its lower side. These features correspond with the sleep-position of the leaves in the species in question, the parts of the epidermis which bear stomata being covered, while the parts free from stomata are not covered during sleep. As has already been stated in the general diagnosis, the occurrence of two subsidiary cells, which are placed parallel to the pore, is characteristic of the stomata of the Mimoseae. This type is occasionally (*Acacia acinacea*, Lindl., *Pithecolobium bigeminum*, Mart.) somewhat obscured, owing to secondary divisions having taken place transversely or obliquely to the direction of the pore. The stomata lie either in the plane of the epidermis, or deeper than the subsidiary cells; deep depression of the stomata with formation of a vestibule has been observed in *Lysiloma* and in the *Acacias* with phyllodes. In the plants last mentioned the guard-cells are very frequently provided with strong thickening-ridges.

The **mesophyll** is bifacial or centric in structure. As in the case of the position of the stomata, the leaf-structure also stands in relation to the shape and size of the leaflets. The large pinnules of *Inga* are bifacial; small narrow leaflets are centric in structure. The mesophyll in the phyllodes of *Acacia*, which are vertical in position, also shows centric differentiation. The following statements may be made regarding special features in the mesophyll. In the palisade-tissue solitary crystals are not very rare; when they are present, the cells concerned are divided up by cross-walls into chambers, each of which contains one crystal, which is usually embedded in a local thickening of the cell-wall. In *Calliandra fasciculata*, Benth., masses of silica have been observed in the palisade and spongy parenchyma. Many species possess a middle layer, distinguished from the remaining layers of the leaf-tissue by the small amount of chlorophyll it contains, and frequently characterized in the dried leaf by brown tanniniferous contents. A middle layer has been observed by Coester in species of *Elephantorhiza, Prosopis, Leucaena, Acacia, Lysiloma, Mimosa, Calliandra* and *Pithecolobium*. In the phyllodes of *Acacia* it consists

of cells with rather thick, pitted walls. Another peculiarity of the mesophyll is the occurrence of sclerenchyma-fibres. These elements are connected with the sclerenchyma of the veins, and are either abundantly developed, traversing the whole of the mesophyll and spreading out below the epidermis on both sides, or are only scantily developed, penetrating but slightly into the leaf-tissue.

Coester met with sclerenchyma-fibres of the first kind in the following species: *Inga flagelliformis*, Mart., *I. heterophylla*, Willd., *I. lateriflora*, Miq., *I. longiflora*, Spruce, *I macrophylla*, H. et B., *I. marginata*, Willd., *I. myriantha*, Poepp. et Endl., *I. nitida*, Willd., *I. obtusata*, Spruce, *I. quaternata*, Poepp. et Endl., *I. sertulifera*, DC., *I. setifera*, DC, *I. splendens*, Willd., *I. stipularis*, DC., *Pithecolobium auriculatum*, Benth. and *P. campestre*, Benth.; those of the second kind in: *Affonsea juglandifolia*, St. Hil., *Calliandra tenuiflora*, Benth., numerous species of *Inga*, e.g. *I. affinis*. DC., *Parkia oppositifolia*, Spruce, *Prosopis spicigera*, L., *P. Stephaniana* Kth., *Schrankia uncinata*, Willd., *Stryphnodendron coriaceum*, Benth.

The smaller **veins** of the leaf, except in a few cases, are embedded in the mesophyll. Vertical transcurrence of these veins by means of thin-walled tissue is described by Coester only in *Plathymenia*, *Xylia*, and *Calliandra leptopoda*, Benth., transcurrence by means of sclerenchymatous tissue only in *Stryphnodendron coriaceum*, Benth. Sclerenchyma accompanying the vascular bundles of the veins is nearly always developed (with the single exception of *Pentaclethra macrophylla*, Benth.), and usually encloses them as a ring. Enlarged terminal tracheides are found especially within the genera *Adenanthera* and *Piptadenia*. The system of veins in the phyllodes remains to be shortly discussed. Their vascular bundles (as is also frequently the case in petioles) form a ring, which is compressed in correspondence with the flattening of the phyllode; a transverse section of a phyllode shows two rows of bundles, which lie in pairs opposite one another, with their xylem-portions turned towards one another, whilst they usually border directly on the epidermis by means of the mass of sclerenchyma opposite their bast-portions.

The **hairy covering** (Fig. 65) consists of clothing and glandular hairs. It is noteworthy that Coester met with glandular hairs as a constant feature, that two-armed hairs, which have been observed here and there in the remaining Leguminosae, do not occur in this sub-order, and (a still more important point) that the characteristic simple uniseriate hairs with one or several short basal cells and a long terminal-cell, i.e. the type so widely distributed in the Papilionaceae, do not occur either. The clothing hairs may be subdivided into two groups, viz. simple and compound forms. The simple trichomes, which will be discussed first, are unicellular or uniseriate hairs; in the latter case the division-walls are thin. The simple hairs are of varied length and shape. The more peculiar forms will alone be mentioned here. The simple hairs of *Albizzia fastigiata*, E. Mey., are characterized by the fact that the bulbous base of the hair exhibits several thin division-walls. Unicellular one-armed hairs, with a rounded swelling in place of a second arm, are found in species of *Xylia* and *Inga*; unicellular bracket-hairs, with their ends curved like hooks, in *Calliandra lanata*, Benth., and *C. dysantha*, Benth. var. The epidermal cells, surrounding the simple hairs, are occasionally (Ingeae) differentiated like subsidiary cells. In *Affonsea juglandifolia*, St. Hil., the subsidiary cells, which surround the basal part of the hair and are grouped like a rosette, have cystolith-like thickenings, which are constituted and orientated just like those so well known in subsidiary cells of the trichomes of the Boragineae, but, unlike the latter, are not impregnated with carbonate of lime. The compound trichomes (shaggy hairs) occur specially in species of the genus *Mimosa*, in which they had previously been found by A. Weiss, and investigated by him with regard to their development. In the simplest case these shaggy hairs

consist of numerous sclerosed fibrous cells, which cover one another like the tiles of a roof; from the middle of the whole structure a long terminal bristle projects; the tips of the lateral fibres are either adpressed to the hair (species of *Mimosa* belonging to the section *Eumimosa*, *M. adversa*, Benth., *M. camporum*, Benth., and *M. cruenta*, Benth.), or are curved round into the form of a hook, or project outwards (*M. calycina*, Benth., *M. Claussenii*, Benth., *M. debilis*, H. et B., *M. dimidiata*, Benth., *M. Gardneri*, Benth., *M. hypoglauca*, Mart., *M. imbricata*, Benth., *M. obtusifolia*, Willd., Fig. 65, *A*,

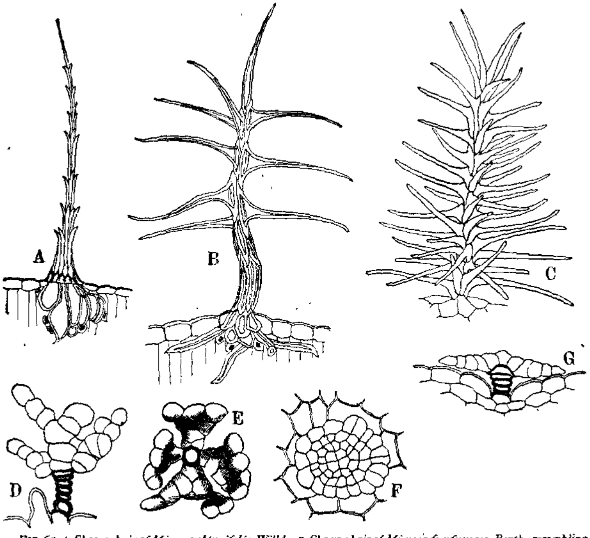

FIG. 65. A, Shaggy hair of *Mimosa obtusifolia*, Willd.; B, Shaggy hair of *Mimosa furfuracea*, Benth., resembling a fir-tree. To the base of both of these sclerenchymatous cells are attached, which, penetrating into the mesophyll, anchor the hair firmly, and are accompanied by crystal-cells (crystals shaded). C, Shaggy hair of *Mimosa incana*, Benth., resembling a fir-tree. D–E, Branched glandular hairs of *Mimosa Spruceana*, Benth.; E, Gland seen from above. F–G, Peltate gland of *Mimosa punctulata*, Spruce.—Original.

M. Radula, Benth., *M. rigida*, Benth., and *M. subsericea*, Benth.). In other cases a multiseriate group forms a columnar mass, from which at certain definite distances 4–6 long ray-cells project, forming a more or less distinct whorl in each case. The following species possess these shaggy hairs, branched like a fir-tree: *M. aurivillus*, Mart., *M. calothamnus*, Mart., *M. furfuracea*, Benth. (Fig. 65, *B*), and *M. sordida*, Benth. If one imagines the interspaces between the whorls in these abietiform shaggy hairs reduced, the tufted shaggy hairs, in part also abietiform and found in *Mimosa calodendron*, Mart., *M. incana*, Benth. (Fig. 65, *C*) and *M. verrucosa*, Benth., would result. The different shaggy hairs, which have just been discussed, are often further characterized by the fact that they have a sclerosed foot, which penetrates

deeply and sometimes like a root into the mesophyll (see Fig. 65, *A–B*). The last category of compound trichomes is represented by simple tufted hairs, which consist of simple unicellular hairs placed side by side; these have been observed by Coester in *Pentaclethra macrophylla*, Benth., and *Prosopis Stephaniana*, Kth.

The glandular hairs likewise exhibit different forms. In the first place mention may be made of glandular hairs with a uniseriate stalk of variable length and an ellipsoid multicellular head, of variable size, divided by horizontal and vertical walls. External glands of this type are the most widely distributed in the Mimoseae; Coester met with them in most of the genera (*Parkia, Entada, Piptadenia, Stryphnodendron, Adenanthera, Elephantorhiza, Gagnebina, Prosopis, Neptunia, Desmanthus, Mimosa, Schrankia, Leucaena, Xylia, Acacia, Lysiloma, Calliandra, Albizzia, Pithecolobium, Enterolobium, Serianthes, Inga, Affonsea*). A second category of external glands comprises those with a peltate head of variable size. Among these we may first class the peltate glands of some *Mimosas* (*M. cylindracea*, Benth., *M. millefoliata*, Scheele, *M. myriadena*, Benth., and *M. punctulata*, Spruce, Fig. 65, *F–G*), which are shortly stalked and are sunk in pit-like depressions of the leaf-surface; the shield of these glands usually consists in places of two layers of cells and in surface-view shows numerous isodiametric cells, which, on the one hand, are arranged in concentric circles, and, on the other hand, may often be subdivided into 5–7 sectors, limited by an equal number of radii; in *M. myriadena* the shield attains a diameter of ·14 mm. With these we may group smaller external glands, which are likewise sunk in small pits in the leaf, are very shortly stalked, and have a capitate or peltate glandular portion, divided exclusively by vertical walls. Coester observed glands of this kind, provided with a head of few cells, in *Acacia dodonaeifolia*, Willd., *A. exsudans*, Lindl., and *A. leprosa*, Sieb., while others composed of more numerous cells and having a considerable accumulation of secretion below the cuticle, are present in some *Mimosas* (*M. hostilis*, Benth., *M. interrupta*, Benth., *M. malacocentra*, Mart., *M. opthalmocentra*, Mart., *M. sericantha*, Benth., and *M. verrucosa*, Benth.). Peculiar glandular structures, which may be described as branched or palmately divided glandular hairs, occur on the lower side of the leaf of *Mimosa Spruceana*, Benth. (Fig. 65, *D–E*). They consist of a uni- or biseriate stalk, which often broadens out upwards, is composed of short cells, and divides into 4–6 branches of no great length, the branches being blunt at their tips, and usually grouped together in a tufted manner, or more rarely spread out in the form of rays. Lastly, glandular shaggy hairs with a multiseriate stalk and a spherical or obconical head, composed of numerous cells, occur in certain species of *Mimosa* (*M. adversa*, Benth., *M. foliolosa*, Benth., *M. paludosa*, Benth., *M. somnians*, H. et B., *M. triquga*, Benth.); a transition to these hairs is afforded by glandular hairs with a similarly constituted head, but with a uniseriate, though fairly long stalk (*M. brevipinna*, Benth., *M. dolens*, Vell., *M. Franciscana*, Benth.). Having described the true glandular hairs, it remains to be mentioned that rather large peltate or wart-like masses of tissue occur on the petiole in most Mimoseae; these are visible even with the naked eye, have secretory functions and, as they are easily observed, have already been described by systematists (see Delpino). Without dealing more fully with the diverse structural features of these petiolar glands, it need only be stated here that they consist of a parenchymatous group of cells, below which bundle-terminations with abundant deposition of crystals in the surrounding tissue usually occur; they are occasionally (in the *Acacias* possessing phyllodes) reduced to glandular spots, and sometimes excrete a sap, containing sugar.

According to Borodin and Coester, solitary crystals are the usual form of excretion of **oxalate of lime**. Clustered crystals have only been observed in the two genera *Mimosa* and *Piptadenia*, and in these only in the leaf, where they accompany the veins and also occur in the mesophyll; they have not been found in the axis in any member of the Mimoseae. The solitary crystals occur both in the form of ordinary rhombohedra, and also of rod-shaped crystals shaped like styloids. In the leaf the crystals are found in the veins as well as in the mesophyll. Both forms occur accompanying the vascular bundles of the veins. In the mesophyll the crystals are found singly in the chambers of septate palisade cells, not uncommonly (as is especially frequent in the Ingeae) embedded in a thickening of the cell-wall. A special peculiarity which occurs in numerous species is the accumulation of crystals below the place of insertion of the hairs, especially the larger ones. In the axis the crystals of the wood and bast are contained in chambered fibres; in the primary cortex they are frequently found enclosed in thickenings of the walls. A fact, which deserves special mention, is the occurrence of small crystal-cells in the pith of species of *Adenanthera, Desmanthus, Dichrostachys*, and *Neptunia*; these cells are usually placed together in groups, which arise from one cell by secondary division.

To conclude the description of the leaf-structure, the special **secretory organs** of the Mimoseae in axis and leaf may be discussed together. They are as follows: (*a*) secretory cells of different kinds, (*b*) tubular elongated cells, which have varied contents and are present especially in the soft bast, and (*c*) intercellular secretory receptacles, in which the secretory space is surrounded by bracket-cells. It is impossible to enter into details here regarding the formation of gum in the *Acacias* (*A. Senegal*, Willd., &c.), which yield gum-arabic. Whilst referring to the works on this subject by Möller (Sitz.-Ber. Wiener Akad., 1875, pp. 219 et seq.) and Lutz (Bull. de la Soc. bot. de France, 1895, pp. 467–471), it need only be remarked that normal elements of the soft bast, pericycle and wood undergo metamorphosis into gum. Coester observed secretory cells in certain species of *Calliandra, Pentaclethra, Pithecolobium*, and *Prosopis*. Firstly, the secretory cells of *Calliandra*, which have been observed only in *C. Harrisii*, Benth., *C. surinamensis*, Benth. var. *tenuiflora*, Benth., and *C. trinervia*, Benth., and give rise to transparent dots, occur in the spongy parenchyma; they are fairly large and contain a colourless secretion, which is readily soluble in water. In *C. Harrisii* they are only to be found at the margin and in the tips of the leaflets; in the remaining species they are scattered through the whole leaf. Secretory cells with wide lumina, lying in groups in the neighbourhood of the veins, characterize *Pithecolobium cauliflorum*, Mart., and *P. inaequale*, Benth., as well as *Pentaclethra filamentosa*, Benth.; their colourless or yellow secretion is for the most part soluble in water. *Prosopis juliflora*, DC. and *P. Nandubey*, Lorentz, both belonging to the section *Algarobia*, DC., possess special secretory cells. In these plants tubular or rounded secretory cells, which have yellowish contents and are specially characterized by the gelatinization of their cell-walls, are found in all parts of the mesophyll. The secretory receptacles of the second type, the tubular secretory cells of the soft bast, exactly correspond to the tannin-sacs, which were very fully discussed in the Papilionaceae. Like the latter, they have wide lumina, are usually elongated considerably in the vertical direction, are arranged in longitudinal series, and do not always contain brown tanniniferous masses in their contents, but very varied secretions, which are either completely free from tannin and colourless, or (in the young shoots of *Mimosa sensitiva*, *M. prostrata*, and *M. floribunda*, according to Trécul) resemble latex. According to Coester, the contents of the sacs which occur in many species of *Mimosa*, and which on account of their width can be followed into the vascular

bundles of the leaf in these plants, are completely free from tannin. Sacs which from the morphological point of view are identical with the above, according to Haberlandt, form the tissue-system which conducts the stimulus in *Mimosa pudica*; the cell-sap of these sacs, according to the same investigator, contains a gummy or mucilaginous substance, a compound of the nature of a glucoside and resinous granules. With regard to the sacs of *Mimosa pudica*, we may also mention that, according to Haberlandt, they possess in the living condition a protoplasmic lining layer with a very large nucleus and on each cross-wall exhibit one large pit, the pit-membrane of which is traversed by protoplasmic threads. No statement as to the occurrence of similar pits in the sac-cells of other Mimoseae is known to me in the literature. According to Coester, the secretory or glucoside-containing sacs in question have a wide distribution in the sub-order. The third form of special secretory organs has only been observed in *Pithecolobium divaricatum*, Benth. and *P. glomeratum*, Benth. In the upper part of the spongy parenchyma in these two species there are intercellular secretory receptacles, in which the secretion, as in certain species of the Papilionaceous genus *Lonchocarpus*, is surrounded by bracket-cells, which are not in lateral contact, and do not completely shut in the secretory space.

The structure of the **petiole** has only been investigated in species of *Acacia* and *Mimosa*. In the characteristic region the fibro-vascular system consists of a continuous or interrupted ring of bundles, with which two additional lateral bundles are occasionally associated on the upper side.

3. STRUCTURE OF THE AXIS. The structure of the wood has been investigated in detail by Möller, Solereder, Saupe and Coester, the structure of the cortex by Möller and Coester.

Regarding the structure of the **pith** there is little to be said. As a rule it consists of lignified cells. The medullary cells of aquatic species, belonging to the genera *Desmanthus*, *Dichrostachys*, *Mimosa* and *Neptunia*, have unlignified cell-walls. In these plants lacunae also occur in the pith. Medullary vascular bundles with central soft bast and peripheral xylem, almost destitute of vessels, have been observed in *Elephantorhiza Burchellii*, Benth., sclerosis of the central part of the pith in *Albizzia amara*, Boiv.

The **xylem** consists of vessels with lumina of various sizes, medullary rays, which are mostly narrow[1], wood-prosenchyma with simple pits and wood-parenchyma. According to Saupe, tracheides have not been found in any member of the sub-order. The vessels have simple perforations throughout and show bordered pits even on those portions of their walls which abut on parenchyma. Sieve-like pits have been observed on the walls of the vessels in species of *Acacia*, *Adenanthera*, *Inga* and *Mimosa*. The medullary rays are built up of low cells, which are elongated in the radial direction and appear small in tangential sections. Höhnel met with tier-like arrangement of the medullary rays in some species of *Inga* and *Acacia*. The development of wood-parenchyma varies. The wood-prosenchyma is frequently characterized by the possession of a gelatinous layer and does not usually have wide lumina. On the other hand, prosenchyma-cells with unusually wide lumina are met with in the wood of *Desmanthus*, *Mimosa Velloziana*, Mart., *M. obovata*, Benth., *Schrankia* and *Leucaena*. Saupe states that fibrous cells, which store up starch, occur in species of *Acacia*, *Desmanthus*, *Inga*, and *Mimosa*; septation of the wood-prosenchyma, combined with storage of starch, is described by Saupe in the case of species of *Acacia* and *Inga*, and by Coester in species of *Neptunia*, *Piptadenia*, *Plathymenia* and *Prosopis*

[1] According to Möller, however, the medullary rays attain a breadth of five cells in *Parkia*.

The following facts may be pointed out with regard to the structure of the **cortex**. According to the concordant results of investigations by Möller, Coester and others the cork always arises superficially, usually in the second or third layer of cells below the epidermis, rarely subepidermally. The mature cork-cells are slightly flattened, but almost cubical. They are occasionally sclerosed on one side (*Acacia*) or thickened on all sides (*Inga*); in other cases they have delicate walls. In the bladder-like swellings of the stem of the floating plant, *Neptunia oleracea*, Lour. (*Desmanthus natans*, Willd.), according to Rosanoff, Scott and Wager and H. Schenck (and contrary to Beck's statements on the subject) aerenchyma arises in the third or fourth layer of cells below the epidermis in place of cork; this aerenchyma dies away towards the end of the period of vegetation, and is replaced by normal cork-tissue. According to H. Schenck, the stems, leaves, and peduncles of *Mimosa cinerea*, Vell., which grow into the water, also possess aerenchyma of subepidermal origin and consisting of radially elongated cylindrical cells, which are free from one another except for small surfaces of contact.—The primary cortex either has thin walls or is collenchymatous, and frequently contains tannin. It is composed of exceptionally large cells in *Parkia filicoidea*, Welw., according to Coester. Stone-cells are rarely present in the primary cortex; thus they occur only in that of *Albizzia anthelmintica*, Brongn., among the cases investigated by Coester. —According to Coester, the outer limit of the bast is always formed by a composite and continuous sclerenchymatous ring, the bast-fibres of which not uncommonly exhibit a gelatinous layer similar to that of the wood-fibres. According to Möller, however, species apparently occur (e. g. *Acacia lophantha*, Willd. = *Albizzia lophantha*, Benth.) which only exhibit isolated groups of bast-fibres in place of the sclerenchymatous ring. In the secondary phloem stratification due to bands of hard bast is not uncommon. Stone-cells also occur in the secondary bast. On the other hand, it is a peculiar phenomenon that the medullary rays which traverse the secondary hard bast, mostly resist sclerosis. According to Möller and Coester, the structure of the sieve-tubes is also characteristic; for scalariform sieve-plates are alone stated to occur and the sieve-cells are said to be universally distinguished by their considerable length (about 1 mm.). The medullary rays not uncommonly broaden outwards in the bast, becoming multiseriate.

Having described the stems with normal structure, we may mention two or three cases of **anomalous stem-structure** which occur in some twining species. A large number of the lianes belonging to the Mimoseae have normal structure, e.g. according to H. Schenck, *Acacia lacerans*, Benth. and *Piptadenia trisperma*, Benth. Other lianes are only anomalous in so far as they possess winged or rather grooved stems; according to H. Schenck this type includes: (*a*) the piece of stem, collected by Schenck under No. 662, which perhaps belongs to a species of *Acacia*, (*b*) *Piptadenia latifolia*, Benth., as well as (*c*) the stem named *Acacia sarmentosa* and described by Coester, which forms part of Eggers' collection of woods (in Herb. Monac.). A true anomaly in the structure of the axis occurs in the genus *Entada*, in which the groundwork of the wood consists of unlignified wood-parenchyma with delicate walls and enclosing vessels, bundles of wood-prosenchyma and strands of sieve-tubes. These latter probably arise secondarily in the parenchyma of the xylem and are not formed directly from the cambium. Krüger was the first to describe this anomaly in the case of a stem of *Entada gigalobium*, collected by Semper in Manila. H. Schenck observed the same anomaly in *Entada scandens*, Benth. and *E. polystachya*, DC., although he is not quite certain as to the occurrence of the strands of sieve-tubes in the wood. Coester recently demonstrated this feature with certainty in a piece of the axis of *Entada scandens* derived from the collection in Zürich.

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ROSACEAE.

1. Review of the Anatomical Features. Constant anatomical characters are almost entirely wanting in this Order. The only points to be mentioned are the following: (1) the lack of simple uniseriate clothing hairs; and (2) the presence of bordered pits in the prosenchymatous groundwork of the wood in almost all woody species. The stomata in nearly all the Chrysobalaneae are provided with two or more subsidiary cells parallel to the pore; in the remainder of the investigated species they are surrounded by several ordinary epidermal cells. The perforations of the vessels are always simple in the Chrysobalaneae, but in the rest of the woody species a tendency to the formation of scalariform perforations has been demonstrated. Cork-formation varies, being either internal (Spiraeeae pro parte, Potentilleae, Poterieae), or superficial (Chrysobalaneae, Pruneae, *Rhodotypus*, *Quillaja*, Pomeae). In the woody species the pericycle either contains isolated groups of bast-fibres or

a composite and continuous sclerenchymatous ring, which in the Chrysobalaneae is partly composed of U-shaped, sclerosed cells. With regard to the structure of the wood, we may mention the varied breadth of the medullary rays, as also the fact that the vessels have lumina of various sizes, and that the wood-parenchyma takes an important part in the formation of the wood in the Chrysobalaneae only. Oxalate of lime is usually excreted in the form of (1) solitary crystals, those of the Pomeae being frequently combined into the form of a widely open V or an I; and (2) clustered crystals; true styloids have been met with in *Quillaja* alone. Silicified cell-membranes and masses of silica in the cell-contents are of frequent occurrence in the Chrysobalaneae. As regards internal secretory organs the abundance of tannin may be especially pointed out. Other noteworthy features are: the occurrence of mucilaginous cells in the epidermis of the leaf (in many species); of mucilage-cells in the parenchyma of the leaf-veins and of the stem (*Neurada, Eriobotrya*); of lysigenous mucilage-canals (in the pith of the branch in *Neurada*); and of secretory cavities (in the leaf of *Lecostemon* and *Couepia bracteosa*, Benth.); gummosis occurs in the wood and cortex of the Pruneae. In the bast of many Chrysobalaneae tannin is localized in special sac-like cells. The hairy covering consists (1) of simple, unicellular trichomes, which are occasionally united into tufted and stellate hairs, or exhibit transitions to two-armed hairs, (2) of peltate hairs (*Lecostemon*), (3) of glandular hairs, and (4) of glandular shaggy hairs. The nectaries on the petiole and leaf-surface and some of the glandular leaf-teeth, which occur in certain species, resemble the glandular shaggy hairs in their structure (in the possession of a secretory palisade-like epidermis).

Special anatomical characters, which are of value in detailed diagnosis, have been observed, viz. the tendency to palisade-like differentiation of the epidermis of the leaf (many Chrysobalaneae), development of hypoderm in the leaf, papillose differentiation of the lower epidermis, occurrence of sclerenchyma-fibres or other spicular cells in the mesophyll (*Lecostemon, Licania, Couepia*), cork-warts on the leaf (*Couepia bracteosa*, Benth.), and septation of the pith without sclerosis (*Prinsepia*).

2. STRUCTURE OF THE LEAF. The leaf-structure has been investigated in considerable detail in the Chrysobalaneae by Küster[1], in the Spiraeae and Potentilleae by Protits, in the Rubeae by Fritsch, and in the Pomeae by Gérard.

The **leaf-structure** is almost always bifacial in the Pomeae; it is centric in *Crataegus Azarolus* only. In the Chrysobalaneae, on the other hand, all the cells of the mesophyll are usually more or less elongated like palisade-tissue, the mesophyll being distinctly bifacial in *Lecostemon* and *Prinsepia* only. Large lacunae, elongated in a direction parallel to the course of the veins, have been met with in the mesophyll of *Couepia bracteosa*, Benth. The **epidermal cells** of the Pomeae have a varying outline in surface-view; a polygonal outline (even on the lower side of the leaf) is, with few exceptions, characteristic of the Chrysobalaneae. In a transverse section of the leaf the epidermal cells of many Chrysobalaneae (species of *Acioa, Couepia, Licania, Moquilea, Parinarium*) are characterized by palisade-like elongation. In some cases the walls of the epidermal cells in the same tribe are thickened in a varied and characteristic manner. A delicate and striated cuticle is described by Gérard in *Chaenomeles japonica*; cuticular prominences, resembling mountain-crests, occur in *Cormus domestica*, whilst elevations of the cuticle are only present round the stomata in *Pyrus communis*. In *Kerria japonica* the epidermis is provided with a coating of wax, which is 5 μ in thickness, and stratified. Papillose differentiation of the lower epidermis is described by Gérard and

[1] Küster investigated all the genera except *Trichocarya* and *Griffonia*.

Folgner in *Cotoneaster buxifolia*, Wall., and *C. microphylla*, Wall. (solid papillae) and by Küster in *Couepia grandiflora*, Benth., *C. Martiana*, Hook. f., *C. Uiti*, Benth., and *Moquilea Turiuva*, Hook. f. According to Radlkofer, Küster, Kruch and others, gelatinization of the inner wall of the epidermal cells occurs in species of *Chrysobalanus, Grangeria, Hirtella, Parinarium, Prunus, Spiraea, Stephanandra, Kerria, Neviusa, Eucryphia, Rubus, Dryas, Potentilla, Chamaerhodos, Agrimonia, Margyricarpus, Acaena, Poterium, Cliffortia, Rosa, Cydonia, Pyrus, Crataegus, Cotoneaster, Photinia, Raphiolepis, Chamaemeles, Amelanchier*, and *Osteomeles*[1]. True **hypoderm** has been observed by Gérard in *Heteromeles arbutifolia* and *Osteomeles cordata*; by Fritsch in the species of the section *Micranthobatus* of *Rubus*, and by Küster in species of *Chrysobalanus, Couepia, Grangeria, Hirtella, Lecostemon, Licania, Moquilea, Parinarium*, and *Parastemon* (in these latter sometimes enclosing mucilaginous cells). The **stomata** of the Chrysobalaneae (exception: *Stylobasium*) and Pomeae (exception: *Crataegus Azarolus*) nearly always occur only on the lower side of the leaf. Whilst the stomata of the Chrysobalaneae (*Lecostemon, Prinsepia* and *Stylobasium* excepted) are provided with subsidiary cells placed parallel to the pore, those of the Pomeae, the guard-cells of which are usually slightly depressed below the level of the leaf-surface, are surrounded by a variable number of ordinary epidermal cells; water-pores are met with on the leaf-teeth of numerous members of the Order, belonging to the genera *Alchemilla, Aremonia, Crataegus, Geum, Potentilla*, &c.

The vascular bundles of the smaller **veins** of the leaf are, if the Pomeae be first taken into consideration, either embedded, and provided with a parenchymatous sheath with (e.g. *Stranvaesia glaucescens*) or without (*Cydonia vulgaris*) sclerenchyma, or they are vertically transcurrent. In the Chrysobalaneae the vascular bundles of the veins are almost throughout (*Prinsepia* and *Stylobasium* excepted) surrounded by a characteristic sclerenchymatous ring, composed of sclerenchyma-fibres and cells sclerosed in the form of a U. Vertical transcurrence of the veins by means of plates of sclerenchyma has been observed among the Chrysobalaneae in *Acioa, Chrysobalanus, Couepia, Hirtella* and *Licania* pro parte. At this point mention may be made of the occurrence of terminal tracheides, with wide lumina, in *Licania* and *Moquilea*, of fibre-like spicular cells, traversing the mesophyll, in *Lecostemon*, and of spicular cells of simpler shape in *Licania micrantha*, Miq., *L. obovata*, Benth., *L. subcordata*, Fritsch and L. *triandra*, Mart., as well as in *Couepia bracteosa*, Benth. (here in relation to the secretory cavities, see below).

Oxalate of lime is usually excreted in the form of solitary and clustered crystals. The solitary crystals, found in the chambered fibres of the bast, as well as in the palisade-tissue of the Pomeae, are frequently combined in a form varying from a widely open V to a styloid-like I. True styloids, however, are known only in the genus *Quillaja*.

The mode of excretion of oxalate of lime, whether as solitary or as clustered crystals, is occasionally characteristic of the smaller groups. Thus, according to Fritsch, within the genus *Rubus* the species of the section *Micranthobatus* only possess simple crystals or clusters consisting of few (3–4) individual crystals; the species of the sections *Anoplobatus, Idaeobatus, Bathothamnus* and *Eubatus* have only clustered crystals, and so on. In *Potentilla* and *Spiraea* clustered crystals are present either exclusively or as the predominant form (Borodin). According to Möller, solitary crystals are prevalent in the primary cortex of the Pomeae, whilst that of the Roseae and Pruneae contains clustered crystals or solitary and clustered crystals; according to the same author, the bast of the Pomeae and of *Rosa* and

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[1] Gérard, as well as Folgner and Lalanne, has interpreted the mucilaginous inner walls in species of *Raphiolepis, Chamaemeles* and *Eriobotrya* as hypodermal cells.

Spiraea, almost without exception, contains chambered fibres with rhombohedra or short columns of the V-shaped type, whereas the bast of the Pruneae usually has isolated crystal-sacs with clustered or solitary crystals. In *Prunus Cerasus*, L., clustered crystals have been observed in the epidermis of the leaf (Virchow), and large solitary crystals (*Stranvaesia glaucescens*, '*Pyracantha vulgaris*') or clustered crystals (*Cydonia vulgaris*) have been met with in the palisade-tissue of some Pomeae (Gérard).

Having dealt with oxalate of lime, we will now discuss the occurrence of **silica** in the Chrysobalaneae, which forms a striking character of this tribe. The silica is deposited in various ways and the following cases were distinguished by Küster: silicified membranes, silica-bodies, silica-plugs, silica-sacs and intercellular deposits of silica.

Silicified membranes are common in the leaves of the genera of the Chrysobalaneae (except *Lecostemon*, *Prinsepia* and *Stylobasium*). The silicification of the cell-wall occurs chiefly in the epidermis of the leaf (whereby the semi-metallic lustre of many leaves is caused), and especially in the neighbourhood of the bases of hairs, where the cell-walls undergo a curious alteration, owing to thickening and silicification, whilst the trichomes themselves are not silicified;—more rarely the mesophyll is involved (to a considerable extent in *Licania parviflora*, Benth. and *Couepia racemosa*, Benth.), and occasionally cells of the primary cortex.

The silica-bodies are siliceous deposits, which originate in the cell as small grains and subsequently increase in size, occasionally to such an extent that they fill the lumen of the cell; deposits of the latter kind can only be distinguished from the silica-plugs to be discussed below, by the fact that the cell-wall surrounding them is not silicified. They are either compact, clear, and transparent structures of spherical or conical shape, or are composed of loose material; those of conical shape occur only in the cells covering the veins. Küster has met with silica-bodies: in the pith, medullary rays and pericycle of the axis and in the neighbourhood of the leaf-veins in all the genera except *Prinsepia*, *Parastemon* and *Stylobasium*, in the epidermis of the leaf in *Lecostemon* and *Couepia bracteosa*, Benth. (in the latter plant, only above the secretory cavities); in the mesophyll in *Lecostemon* and some species of *Couepia* and *Moquilea*; singly in the cells of the peltate hairs of *Lecostemon*. We may include under the same category the deposits of amorphous silica, which occur in 'cauto'-bark and were first described by Crüger; they are of two kinds: viz. silica-bodies with peg-like projections, which are due to the filling of sclerosed cells together with their pit-canals (they have also been met with by Küster in *Chrysobalanus Icaco*, L.), and masses filling up what are called prong-cells, which after burning possess the peculiar property of glistening in the most various colours in reflected light.

The silica-plugs differ from the silica-bodies in the fact that they form an adherent lining to the cell-wall in earlier stages, and owing to growth in bulk finally fill up the entire lumen of the cell with an opaque mass having a gummy appearance; the cell-membrane enclosing this mass is silicified. These silica-plugs are of frequent occurrence in the epidermis and mesophyll of the leaf in all the genera except *Prinsepia*, *Parastemon*, and *Stylobasium*. Those in the mesophyll of *Hirtella* and of species of *Chrysobalanus* occasionally enclose clustered crystals.

The silica-sacs, i.e. cells which have wide lumina and delicate walls, are connected with the upper epidermis by means of hypodermal cells and contain a brittle siliceous secretion in the form of a number of fragments; they are stated by Küster to occur only in the mesophyll of *Licania micrantha*, Miq. and *L. triandra*, Mart.; finally the intercellular masses of silica have only been found in 'cauto'-bark.

Typically differentiated internal **secretory organs** are not a common feature in this Order. Tannin, although very widely distributed, as was first pointed out by Trécul, is but rarely deposited in special receptacles. In many species, tannin-containing cells, showing a special arrangement, occur in the pith, as will be described below; the region of the pith which borders on the wood, as well as the cortical layer external to the bast, and the medullary rays, are usually rich in tannin; lastly, the bast also contains tannin-sacs. The latter, as far as is known to me, are only differentiated as idio-

blasts (in the form of elongated sacs with wide lumina) in the bast of certain Chrysobalaneae (*Couepia*, species of *Moquilea* and *Parinarium*). The tannin-sacs of the Chrysobalaneae are specially remarkable from the fact that at many points their walls are hemispherically protruded or depressed as the case may be, a condition which leads to a dovetailing of the contiguous wide-lumened elements. The mucilaginous epidermal and hypodermal cells of the leaf have already been referred to above. Cells with their membranes mucilaginous on all sides were met with by Volkens in *Neurada procumbens*, L.; they accompany the vascular bundles of the veins, and occur at the margin of the pith, in the medullary rays, and at the inner margin of the primary cortex. The mucilage-cells described by Gérard as 'cellules hypertrophiées incolores,' are found in the parenchyma of the large veins and in the primary cortex of *Eriobotrya japonica*, Lindl., while the mucilage-cells observed by Folgner occur in the spongy parenchyma of species of *Pyracantha*. Volkens, moreover, has met with a lysigenous mucilage-canal in the centre of the pith of *Neurada procumbens*. Küster's demonstration of secretory cavities with resinous contents in the leaves of the species of *Lecostemon* and of *Couepia bracteosa*, Benth. (but not in other species of *Couepia*) is of special interest. These cavities are always found in connexion with the upper and lower epidermis, and in *Couepia bracteosa* are accompanied by spicular cells. Finally, the gummosis which occurs in the tissue of the wood and cortex of certain Pruneae may be mentioned. In the wood it always affects previously differentiated groups of parenchymatous cells, 'abnormal wood-parenchyma' (see Tschirch, Angew. Pflanzenanat., 1890, pp. 210–211, and the literature cited there); in the cortex, on the other hand, this is not the case. According to Wiegand, the sieve-tubes form the starting-point of the gummosis in the cortex [1].

The **hairy covering** consists of clothing and glandular hairs. The usual form of the clothing hairs is represented by simple unicellular trichomes; uniseriate clothing hairs have not hitherto been met with. The unicellular clothing hairs show manifold variations in their detailed structure. Specially noteworthy types are (i) the trichomes of *Kerria* and *Neviusa* (Protits), which are provided with characteristic, solid, wart-like projections; (ii) the long hairs of species of *Couepia*, *Licania*, *Moquilea* and *Parinarium*, which have thin walls and produce an arachnoid hairy covering on the leaves; and (iii) the trichomes of *Crataegus crenulata*, Roxb., and species of *Cotoneaster*, which form transitions to variously shaped malpighian hairs (Folgner). In *Chrysobalanus oblongifolius*, Michx., the species of *Potentilla* of the section *Stelligerae* and certain *Rubi*, the simple hairs are grouped into tufted or stellate hairs. Peltate hairs have only been met with in the genus *Lecostemon*; the shield of these hairs has a jagged margin, owing to the projecting ray-cells, which have thin walls and narrow lumina, and each of which contains a silica-body (see above); the ray-cells do not all reach to the central point of the shield. The spines of the *Rubi*, which are pure dermatogen-formations, according to Uhlworm and Delbrouck, as well as the thorns of the *Rosae*, in the formation of which the periblem is especially concerned, may also be included here. Ordinary external glands with a uni- or bi-seriate stalk, and a more or less distinct head, which is of variable size and multicellular or more rarely (certain *Rubi*)

[1] The genus *Eucryphia*, the species of which are described by Bentham and Hooker as 'arbores resinosae,' possesses neither resin-canals nor other secretory receptacles. According to Gilg, the resin, which covers the leaves of certain species, is derived from external glands on the stipules. Meigen's statement as to the occurrence of resin-canals in *Kageneckia angustifolia* is incorrect. According to Guignard (Journ. de bot., 1890, pp. 3 and 21 et seq.) special emulsin-cells, corresponding to the myrosin-cells of the Capparideae and Cruciferae, are wanting in the leaves of *Laurocerasus*; here the emulsin—together with tannin—is localized in the parenchymatous sheaths of the vascular bundles of the veins and also in the thin-walled cells which are enclosed by the arcs of hard bast belonging to the bundles.

composed of one or two cells, have been observed by Küster in *Licania*, by Fritsch in *Rubus*, by Reinke in *Alchemilla*, *Fragaria* and *Sanguisorba*. With these structures we may associate: (i) the glandular shaggy hairs, provided with a stalk of varied length and a spherical or club-shaped head, found on the vegetative and reproductive organs of the *Rosae* and *Rubi*, on the stipules of species of *Prunus* and *Pyrus*, and on the leaf-teeth of species of *Prunus*; (ii) the analogous but almost sessile glandular structures (nectaries) on the petiole of the species of *Prunus*; (iii) the glands on the leaf-base of certain species of *Parinarium*; (iv) the glandular leaf-teeth in species of *Cydonia*, *Crataegus* and *Pyrus*; (v) the large leaf-glands, described by Küster as palisade-glands, which are visible even with the naked eye, and occur in *Acioa*, *Chrysobalanus*, *Couepia* pro parte, *Hirtella*, *Licania*, *Moquilea*; and (vi) the glandular spots on the lower side of the leaf of *Prunus caroliniana* and *Laurocerasus*. A feature common to all these structures lies in the fact that their glandular surface, which either secretes resin or a mixture of gum and sugar (petiolar glands of *Prunus* and glandular spots on the leaves of *Laurocerasus*), is formed by one or two layers of palisade-like cells, beneath which terminations of vascular bundles are usually found; the secretion is formed beneath the cuticle.

The glandular shaggy hairs are emergences; their stalk is usually traversed by a vascular bundle, which mostly penetrates into the glandnlar head as far as the layer of palisade-cells. In the *Rosae* these hairs occur not only on the axis and on the surface of the leaf, but also on the leaf-teeth and occasionally also on the spines (*R. centifolia*, f. *muscosa*). The petiolar glands of *Prunus* are merely glandular shaggy hairs with a short stalk and a large, spherical head, which is somewhat depressed on the upper side. Beneath the palisade-like epidermis of the glands of the Chrysobalaneae, which are most frequently present on the leaf-margin as depressed black spots, 2–3 layers of cuticularized parenchymatous cells are found, and below them the termination of a vein. The latter is wanting beneath the two-layered palisade-like epidermis of the glands of *Laurocerasus*. The secretory leaf-teeth of the species of *Crataegus*, *Cydonia* and *Pyrus* have somewhat diverse structure (see Reinke, loc. cit.), but agree in their epidermis being, in part at least, elongated like palisade-tissue and in enclosing terminations of veins.

Secretory leaf-teeth also occur in other members of the Order (species of *Alchemilla*, *Fragaria*, *Kerria*, *Rubus*, *Sanguisorba*, and *Spiraea*, see Reinke), but these have no palisade-like epidermis; terminations of veins, however, enter the leaf-teeth, and the epidermis frequently (*Alchemilla*, *Fragaria*, *Sanguisorba*, *Spiraea*) contains a group of water-pores.

At this point the cork-warts on the leaf of *Couepia bracteosa*, Benth. may be mentioned; they must not be confounded with the leaf-glands of other Chrysobalaneae already referred to.

The structure of the **petiole** has been investigated by different authors; by Petit in the Rosaceae generally, by Gérard in the Pomeae, by Fritsch in the *Rubi*, by Protits in the Spiraeeae, Kerrieae and Potentilleae, and by C. de Candolle in *Alchemilla*. According to Petit, the most widely distributed condition is the presence of three or five vascular bundles, arranged in the form of an arc, in the characteristic region; e.g. in *Agrimonia*, *Comarum*, *Geum*, *Potentilla*, *Prunus*, *Quillaja*, *Raphiolepis*, *Rosa*, *Rubus*, *Sanguisorba*, *Sorbus* and *Spiraea* pro parte. In other cases this region either contains an arc of wood and bast with both margins rolled inwards (*Couepia*), or an annular system of vascular bundles (*Chrysobalanus*, *Grielum*, *Licania*, *Moquilea*, *Neurada* and *Spiraea* pro parte), which occasionally (*Moquilea guianensis*) encloses a strongly developed vascular bundle with its xylem directed upwards. The number of the vascular bundles, which enter the petiole, is in most cases three; thus Petit gives this number for *Agrimonia*, *Geum*, *Neurada*, *Potentilla*, *Prunus*, *Quillaja*, *Raphiolepis*, *Rosa*, *Sanguisorba*, *Sorbus* pro parte (*S. latifolia*, Pers.) and *Spiraea* (while in *Comarum* and *Sorbus Aucuparia* the number is five); three are described by Fritsch in most of the *Rubi*, by Gérard quite generally

in the Pomeae (with the exception of *Sorbus Aucuparia*), by Protits in *Kerria*, *Rhodotypus* and *Potentilla*, and by C. de Candolle in *Alchemilla*. It may be added that in the petiole of some of the species of *Alchemilla* several rings of wood and bast, enclosing a pith-like tissue, are present in place of the simple vascular bundles.

3. Structure of the Axis. The **cork** originates in various positions (Sanio, J. E. Weiss, Douliot, &c.). It is either superficial, the phellogen being formed from the epidermis or the subepidermal layer of cells, or internal, the place of origin being situated in a deeper layer of the cortex, either on the inner or outer side of the bundles of hard bast belonging to the pericycle, or on the inner side of a variously constituted endodermis.

Superficial cork-formation has been demonstrated: (*a*) with the subepidermal layer of cells as the place of origin, in the whole of the Chrysobalaneae (Küster), in *Prunus* (incl. *Persica* and *Amygdalus*), in *Quillaja*, in *Rhodotypus*, in *Cotoneaster* pro parte, *Photinia* and *Osteomeles* pro parte; (*b*) with the epidermis as the place of origin, in *Rosa* (the subterranean portions, however, have internal cork-formation, according to Douliot) and in *Cydonia*, *Pyrus* (incl. *Malus* and *Sorbus*), *Mespilus*, *Crataegus*, *Amelanchier*, *Cotoneaster* pro parte and *Osteomeles* pro parte.

Internal cork-formation occurs in the following cases, the more exact place of origin of the cork being added in brackets: *Spiraea* (outermost layer of phloem-cells within the endodermis in *S. Filipendula*, &c.; layers on the inner side of the bundles of hard bast, which belong to the pericycle, in *S. opulifolia*, &c.; seventh to ninth row of cells below the epidermis and 8–10 cell-layers distant from the primary hard bast, in *S. sorbifolia*, &c.; layer of cells on the inner side of a suberized endodermis, with horseshoe-like thickenings, 2 or 3 rows of cells internal to which lies the primary hard bast, in *S. chamaedrifolia*, &c.; according to J. E. Weiss); *Kerria* and *Neviusa* (within an endodermis, which is situated 1 or 2 cell-layers outside the groups of hard bast of the pericycle); *Rubus* and *Dryas* (immediately external to the hard bast of the pericycle); among the Potentilleae in the genera *Geum*, *Coluria*, *Fragaria* and *Potentilla* with *Comarum*, and among the Poterieae in the genera *Alchemilla*, *Agrimonia*, *Acaena*, *Poterium* and *Sanguisorba* (in these generally on the inner side of an endodermis, which forms the boundary of the primary cortex). In accordance with the above statements it appears that superficial formation of cork may be especially characteristic of the Chrysobalaneae, Pruneae, Roseae and Pomeae, internal cork-formation of the remaining tribes investigated; this result, however, requires further confirmation.

Some other peculiarities of the periderm of certain species remain to be discussed. In *Osteomeles cordata*, in which the cork arises subepidermally, the epidermis peels off and the outermost layer of cork-cells undergoes papillose differentiation (Gérard). In many herbaceous genera (*Potentilla*, *Comarum*, *Sanguisorba*, *Agrimonia*, *Fragaria*, *Geum*, *Spiraea*) the tissue produced by the cork-cambium also includes cellulose-cells (termed phelloid cells), which are occasionally even more numerous than the suberized cells. In this case the cork-cells are seen to form tangential rows between the phelloid-cells, and, prior to their complete suberization, appear similar to endodermal cells, in which Caspary's dark dots can be recognized on the radial walls. In *Comarum palustre* and *Poterium Sanguisorba* (both marsh-plants) there are small intercellular spaces between the phelloid cells, indicating a point of agreement with aerenchyma. According to J. E. Weiss, in a certain number of the genera which possess phelloid-cells (namely, those mentioned above excepting *Spiraea*), the sequence of divisions in the formation of the cork differs from what is usual. In these plants a cell is cut off internally by the first tangential wall; it remains in a resting condition for some time, and only subsequently becomes the mother-cell of a second lamella of cork; in the outer cell 1–10 divisions take place in the normal order, and, of the cells thus formed, only the innermost cell and the inner-most but one become suberized, whilst the remaining cells remain unsuberized. Regarding the nature of the cork in the woody species, Möller states that the cork-cells mostly have delicate walls and are occasionally sclerosed on their outer sides in the Pomeae. Phelloderm has been met with in many members of the Order.

The outer portion of the **primary cortex** is frequently collenchymatous in the woody species; occasionally (species of *Osteomeles* and *Aria* according to Gérard) the cortex includes groups of stone-cells, and in *Prinsepia* and

Stylobasium it contains palisade-parenchyma. The endodermis in the herbaceous species has already been discussed in the description of the cork. The pericycle of the woody genera contains primary bundles of hard bast, which become united to one another by means of stone-cells either locally (in species of *Chaenomeles, Crataegus, Osteomeles, Sorbus* and *Stranvaesia*) or completely (in Chrysobalaneae, except *Prinsepia* and *Stylobasium*, species of *Rubus* of the section *Malachobatus*); in the Chrysobalaneae these stone-cells are thickened only on one side, the thickening having in transverse section the form of a horseshoe. According to Gérard and Möller secondary hard bast is developed in many members of the Order, and according to Küster occurs in the Chrysobalaneae. The variously constituted fibres (see Möller) which compose it are either irregularly distributed (Amygdaleae), or form bundles or small tangential plates (*Cotoneaster, Crataegus, Cydonia, Quillaja, Rosa*) or connected cylinders arranged concentrically (*Mespilus, Pyrus, Sorbus, Spiraea*). In *Moquilea*, according to Möller, the secondary hard bast is replaced by groups of stone-cells.

The following statements regarding the structure of the **wood** are essentially based on my earlier investigations [1]. The breadth of the medullary rays and the size of the lumina of the vessels vary. The Chrysobalaneae, for instance, have narrow medullary rays throughout (Küster), while in species of *Rosa, Rubus, Spiraea* and *Kerria*, broad medullary rays have been observed. In the Chrysobalaneae, the lumina of the vessels have a diameter which does not exceed ·03 mm., while in *Rosa canina*, for instance, they attain a diameter of ·15 mm., and so on. The diameter of the bordered pits on the vessel-walls varies between ·003 and ·006 mm. Bordered pitting is usually also found on the wall of the vessel where it is in contact with parenchyma; only in *Hirtella* and other Chrysobalaneae do simple pits occur in these places in addition to the bordered pits. Spiral thickening of the pitted vessels has been observed in species of *Prunus, Kageneckia, Cliffortia, Rosa, Cydonia* (with *Chaenomeles*), *Pyrus* (with *Sorbus, Micromeles*), *Mespilus, Cotoneaster, Photinia* (with *Eriobotrya*), *Raphiolepis, Amelanchier* (with *Aronia*). In the Chrysobalaneae the perforations of the vessels are exclusively simple (Küster); on the other hand, in the whole of the Rosaceae investigated by me, with the exception of the Chrysobalaneae, and in *Quillaja* according to Gilg, scalariform perforations are present (at least in the neighbourhood of the primary wood), in addition to the predominant simple (circular or elliptical) perforations. The number of bars in the former is either very large (*Quillaja*), considerable (*Neillia*), or small (*Kageneckia*). Scalariform perforations rarely (*Neillia, Quillaja*) occur also in the secondary wood. The tendency to the formation of scalariform perforations in this Order (excluding the Chrysobalaneae) also shows itself in the occurrence of special modifications in certain species. In *Quillaja*, combinations of both forms of perforation are found, the middle of the scalariform perforation showing a simple circular opening; in *Spiraea ulmifolia*, Scop., simple elongated elliptical perforations occur; in *Potentilla fruticosa*, L., *Cydonia vulgaris*, Pers. and *Sorbus Aucuparia*, L., there are circular perforations with a network of bars. The lumen of the vessel has been observed to be filled with silica in the plant which forms the source of

[1] These extend to species of *Chrysobalanus, Hirtella, Prunus, Amygdalus, Neillia, Spiraea, Stephanandra, Kageneckia, Rubus, Potentilla, Cliffortia, Rosa, Crataegus, Cydonia, Sorbus*; see also Möller, Chalon and Burgerstein, ll. cc. The results of the careful investigations of the last-named author cannot be entered into in detail, especially as they only have reference to relatively thick parts of the axis. These researches extend especially to numerous species of the following genera of Pomeae: *Pyrus, Mespilus, Crataegus, Cotoneaster, Photinia, Stranvaesia* and *Amelanchier* (sensu Durand), and conclude with a table for their determination, in which the occurrence or absence of tertiary thickening-layers in the vessels and tracheides, the breadth of the vessels, the height of the medullary ray-cells, the number of the medullary rays to the mm. (in a transverse section) and the number of rows of cells in the medullary rays (in a tangential section) form the characters.

Cauto-bark (Küster), and with carbonate of lime in the heart-wood of *Sorbus torminalis* and *Pyrus microcarpa* (Molisch). Apart from the Chrysobalaneae, wood-parenchyma is little developed. In the Chrysobalaneae it either forms tangential bands, or even the chief part of the wood. The walls of the prosenchymatous groundwork of the wood as a rule bear bordered pits, and are occasionally (species of *Stephanandra, Rosa, Cydonia, Chaenomeles, Mespilus, Crataegus*) also provided with a spiral band. Among the Chrysobalaneae Küster describes simple pitting of the prosenchyma in *Stylobasium* only; side by side with the wood-fibres bearing bordered pits, others with simple pits are sometimes (*Spiraea, Kerria, Rhodotypus* and *Potentilla*) found in subordinate quantity; the latter are provided with delicate division-walls in *Spiraea ulmifolia*. Lastly, mention must be made of the occurrence in *Ferolia guianensis*, Aubl. of a xylem-mass with a tier-like structure (involving the medullary rays) (Höhnel).

According to Gris and others, the **pith** is either homogeneous (*Cydonia, Pyrus* pro parte,—namely *P. communis*,—*Photinia*, incl. *Eriobotrya, Amelanchier*) or heterogeneous (*Spiraea, Rubus, Rosa, Pyrus* pro parte,—namely *Pyrus malus*,—and species of *Sorbus, Mespilus* and *Crataegus*). In the latter case, the peripheral part of the pith is formed of active cells with fairly small lumina and thick walls, while the central part is occupied by empty cells with larger lumina and thinner walls in addition to active cells of the structure described. The active cells of the interior of the pith frequently contain tannin, and in that case are arranged in rows, which are occasionally (species of *Spiraea* of the section *Eubatus*, certain species of *Rosa*) distributed in a reticulate manner among the remaining active cells. The different modes of arrangement of the tannin-cells in the pith have been made use of by Fritsch for systematic purposes in the species of *Rubus*. The pith of the Chrysobalanean genus *Prinsepia* is characterized by a special structure, i. e. septation of the pith without sclerosis.

Note.—With regard to the structure of the **root** it may be mentioned that in many genera the layer of cells situated immediately outside the endodermis is provided with ridge-like thickenings on the radial and transverse walls (Van Tieghem's 'réseau sus-endodermique'). According to Van Tieghem and Russow these are found in *Prunus* incl. *Amygdalus* and *Cerasus, Nuttalia; Spiraea, Exochorda, Gillenia, Kerria, Rhodotypus, Neviusa; Rubus, Dryas, Sieversia, Waldsteinia* pro parte, and *Sibbaldia* pro parte; *Agrimonia, Acaena, Sanguisorba; Rosa; Cydonia* incl. *Chaenomeles, Pyrus* incl. *Malus* and *Sorbus, Mespilus, Crataegus, Cotoneaster, Photinia* incl. *Eriobotrya, Raphiolepis, Stranvaesia* and *Amelanchier*.

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SAXIFRAGACEAE.

1. Review of the Anatomical Features. Only a few features common to all the members of the Order are present, but, on the other hand, there are numerous anatomical characters for groups and species. A tendency to the formation of scalariform perforations in the vessels is peculiar to all the woody genera, since scalariform perforations are always present, either exclusively or side by side with simple openings. In most members of the Order there is no special type of stoma; only in *Dichroa*, *Donatia*, *Quintinia*, and certain groups of species of *Hydrangea* are subsidiary cells found, which are placed parallel to the pore. With regard to the general structure of the wood in the woody species, it may be noted that the medullary rays vary in breadth, that the vessels of the wood have a maximum diameter which varies between ·04 and ·06 mm., that the walls of the vessels, where they are in contact with parenchyma, exhibit large simple or bordered pits, that the wood-parenchyma is little developed, and that the wood-prosenchyma either has bordered or simple pits or both. As regards the origin of the cork, external (in *Peltiphyllum*, Engl., *Vahlia*, the Cunonieae, the Escallonieae, with the exception of *Escallonia*) as well as internal cork (in most of the Saxifrageae, in the Francoeae, Philadelpheae, Hydrangeae, Ribesieae and in *Escallonia*) is found. The boundary of the bast and primary cortex exhibits a very varied structure. Bast-fibres in the secondary bast are rare. The nature of the hairy covering is variable. Simple unicellular hairs have been observed in the Philadelpheae, Hydrangeae, Cunonieae, Escallonieae and species of *Ribes*; simple uniseriate hairs in *Saxifraga*; tufted hairs in *Cornidia*, *Pileostegia*, *Callicoma* and *Broussaisia*; unicellular semi-malpighian hairs in *Abrophyllum*; true malpighian hairs in *Argophyllum*, *Deinanthe*, *Colmeiroa*; unicellular stellate hairs

in *Deutzia* (Fig. 68, *B–C*); lastly, shaggy hairs in *Astilbe*, *Boykinia*, *Heuchera*, *Peltiphyllum*, *Saxifraga*, *Tiarella* and *Tolmiea*. The hairs just referred to, which occur in the Philadelpheae and the Hydrangeae, in *Cornidia* and *Pileostegia*, in *Deinanthe* and *Deutzia* are calcified. A number of other trichomes possess glandular functions, e.g. glandular hairs with a uniseriate stalk of variable length, and a multicellular glandular head (*Saxifraga* and other Saxifrageae), glandular hairs with a uniseriate stalk and a unicellular glandular head (*Francoa*, *Tetilla*, *Vahlia*), glandular shaggy hairs (*Escallonia* Fig. 68, *D*, *Ribes*, *Ceratopetalum*, *Saxifraga* and other Saxifrageae), small glandular hairs, composed of few cells (*Abrophyllum*), peltate glandular hairs (*Quintinia*, *Bergenia*). The external glands of *Cephalotus* (Fig. 69), which occupy an isolated position with regard to their structure, are not hair-like. Oxalate of lime is excreted in various forms, viz. as raphides (Hydrangeae), styloids (*Cornidia*, *Escallonia*), clustered crystals (Saxifrageae, Escallonieae pro parte, *Ribes*, *Philadelphus*, *Carpentiera*), ordinary solitary crystals (*Bauera*), solitary and clustered crystals (Cunonieae, Escallonieae pro parte), and lastly as crystal-sand (*Abrophyllum*). Among the secretions present we may mention in the first place the mucilaginous epidermal cells, found in the leaves of all Cunonieae hitherto investigated. *Abrophyllum* has a ring of laticiferous sacs in the pericycle of the axis. Resiniferous intercellular systems have been observed in the primary cortical tissue of *Roussea*, *Donatia* and *Vahlia* (Fig. 67), secretory cells, of undetermined nature, in the stem of *Parnassia*, elongated tanniniferous secretory sacs in the epidermis of the leaf of *Lepuropetalon*, *Parnassia*, *Chrysosplenium*, and of the species of *Saxifraga* belonging to the section *Cymbalaria*. In conclusion, some other anatomical features, which have been observed in the Order, may be referred to, viz.: the frequent occurrence of hypoderm on the upper side of the leaf in the woody genera, the occurrence of water-pores and of the chalk-glands (Fig. 66) which are connected with water-pores, in *Saxifraga*, of spicular cells in the leaf-parenchyma (*Pancheria*), and of cork-warts on the surface of the leaf (*Cornidia*, *Roussea*), and lastly the development of medullary (species of *Saxifraga*; *Rodgersia*) or of medullary and cortical (*Peltiphyllum*) vascular bundles.

In the special part which follows, the structural features of the leaf and axis in the Saxifrageae and Francoeae are, for reasons of convenience, discussed separately from those of the remaining tribes, and the anatomy of the anomalous genus *Cephalotus* is taken last.

A. Saxifrageae and Francoeae.

2 A. Structure of the Leaf[1]. The **leaf-structure** varies. Within the genus *Saxifraga*, for example, the mesophyll is differentiated into palisade and spongy parenchyma in *S. ciliata* and *S. lingulata*, while in *S. caesia* it is uniform and composed of rounded cells. Thouvenin describes the occurrence of bifacial leaf-structure in species of *Zahlbrucknera*, *Tellima*, *Mitella*, *Tiarella*, *Heuchera*, *Astilbe*, *Hoteia* and *Chrysosplenium*, of centric structure in *Vahlia*, while *Donatia magellanica* has the same character as *S. caesia*. The lateral walls of the **epidermal cells** are undulated or straight. A special feature is presented by the differentiation of the epidermis of the leaf in the species of *Saxifraga* belonging to the section *Cymbalaria*, in the monotypic genus *Lepuropetalon*, in *Parnassia palustris*, and in *Chrysosplenium alternifolium* and *C. oppositifolium* (according to Engler, Thouvenin and Zopf), where long vermiform cells with tanniniferous contents are present between the ordinary epidermal cells of these plants. These **tannin-sacs** occasionally even project above the level of the surface of the remaining epidermal cells, and, as their

[1] Most important literature: Thouvenin and Leist, ll. cc.

contents become brown when the plant withers or is dried, they can often be recognized with the naked eye in herbarium-material as small brown striae. According to Engler, they are produced by fusion in *Saxifraga*, but not so in *Parnassia*, according to Thouvenin.

The **stomata** frequently occur on both sides of the leaf. They are usually surrounded by a variable number of epidermal cells, which are occasionally distinguished from the other cells by their smaller size. A special orientation of the cells adjoining the stomata has been observed only in *Donatia magellanica*; here four such cells are present, the two smaller of which are placed parallel to the pore.

The distribution of the stomata within the genus *Saxifraga* is often very peculiar. While in *S. Huetiana*, *S. hirsuta*, *S. rotundifolia*, and the most nearly allied species no stomata are, according to Leist, met with on the upper side of the leaf, in *S. Cotyledon*, according to the same author, only that portion of the leaf situated nearest to its tip bears stomata, but on both sides; in *S. caesia* and its allies stomata occur only on the margin of the leaf; in *S. bronchialis* they occupy the middle of the upper side of the leaf, whilst on the lower side they are to be found only at the margin. The distribution of the stomata in the genus *Chrysosplenium* is of systematic value (Borodin) in a different way. All the *Alternifolia* have stomata on the lower side of the leaf only, the species of *Dialysplenium*, on the other hand, have them on both sides. In addition to this, the stomata of the *Alternifolia* are arranged in groups. Moreover, according to Thouvenin, the tendency to form groups of stomata is also exhibited by certain *Saxifragae*, most distinctly by *S. sarmentosa*, in which the stomata accompanied by undulated epidermal cells with fairly small lumina occupy the surface of lenticular prominences on the leaf-surface, while the intervening epidermis is composed of cells with straight lateral walls. Licopoli described these groups of stomata in *S. sarmentosa* as glands; Treviranus had previously observed them.

In addition to the true stomata **water-pores** have been observed, especially in the species of *Saxifraga*, and also in *Chrysosplenium* (Borodin), *Tellima grandiflora* (Reinke), and in *Mitella* and *Heuchera* (De Bary).

The water-pores have been examined most thoroughly in Saxifraga. They occur on the upper side of the leaf, viz. always above the terminations of veins or above their glandular epithema, which is usually clearly developed. In certain species of *Saxifraga*, e. g. *S. Aizoon*, the water-pores occur at the base of the leaf-teeth; in the palmately lobed leaves of *S. geranioides* each lobe bears a pore, and in the linear leaves of certain species there is only one pore at the tip of the leaf. In many cases the water-pores lie in the same plane as the rest of the epidermal cells; in other cases they lie at the bottom of pit-like depressions in the surface of the leaf. Pits, the base of which is occupied by water-pores, constitute those organs which have been termed chalk-glands (Fig. 66) in the *Saxifragae*. For from the solution of bicarbonate of lime, which the water-pores secrete, carbonate of lime becomes deposited in the pits by the action of the air (Licopoli), and not only fills the depression, but occasionally forms scales which cover considerable portions of the surface of the plant, and are visible even with the naked eye. Naturally the quantity of lime excreted stands in relation to the chemical nature of the soil in which the plant in question grows; thus it may happen that individuals of the same species from different habitats may have a different appearance so far as their calcareous covering is concerned. The chalk-glands in question occur on the crenations of the leaf-margin in the species of the section *Euaizoonia*, Schott, on the upper side of the leaf in the species of the sections *Kabschia*, Engl., and *Porphyrion*, Tausch; in the latter case several are occasionally (e. g. in *S. caesia*) found in a row along both margins, whilst an odd one occurs near the apex of the leaf.

The **hairy covering** of the Saxifrageae and Francoeae does not show the same variety as that of the woody genera. In *Saxifraga* simple uniseriate hairs are common, and also clothing hairs of the shaggy type, composed of two or more rows of cells, and often reduced to a breadth of one cell at the apex. Two kinds of glandular hairs are found in *Saxifraga*: (1) glandular hairs with a uniseriate, short (*S. geranioides*) or long (*S. tridactylites*) stalk and

multicellular head; and (2) glandular shaggy hairs with a multiseriate stalk and multicellular head. According to Engler, multicellular uniseriate hairs are characteristic of the sections I–VI of his system of classification, multicellular multiseriate hairs of sections VII–XIII. Engler also describes the latter type in the genera *Astilbe*, *Boykinia*, *Heuchera*, *Peltiphyllum*, *Tiarella* and *Tolmiea*. According to Thouvenin, *Francoa*, *Tetilla* and *Vahlia* have glandular hairs, with a uniseriate stalk and a unicellular glandular head, while glandular shaggy hairs, like those of *Saxifraga*, have been observed by the author in species of *Astilbe*, *Hoteia*, *Mitella*, *Tellima* and *Tiarella*; these hairs are rendered remarkable in *Tellima grandifolia* by the cells of the head projecting as papillae. Finally, according to Engler, the genus *Bergia* is characterized by the possession of multicellular glandular peltate hairs, which are sessile within small depressions, and give the leaf a dotted appearance when viewed with a lens.

Oxalate of lime is excreted in the form of clustered crystals or is absent. In *Saxifraga* it is rare. Apart from the tannin-sacs of the epidermis already discussed, secretory elements have not been observed in the leaf.

The structure of the **petiole** has been investigated by Petit only in one species of *Saxifraga* and one of *Heuchera*; for details Petit's work should be referred to.

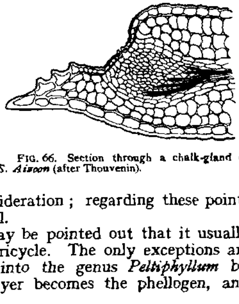

Fig. 66. Section through a chalk-gland of *S. Aizoon* (after Thouvenin).

3 A. Structure of the Axis. The structure of the axis in the tribes under consideration will only be quite briefly treated, as we are dealing with herbaceous plants and the manifold variations in stem-structure, as exhibited by the differentiation of the cortex, the structure of the endodermis, the occurrence or absence of a sclerenchymatous sheath, and the structure of the ring of vascular bundles, cannot be taken into detailed consideration; regarding these points see the works of Thouvenin, Leist and Seidel.

As regards the formation of cork, it may be pointed out that it usually arises in the outermost cell-layer of the pericycle. The only exceptions are *Saxifraga peltata*, Torr., recently erected into the genus *Peltiphyllum* by Engler, in which the subepidermal cell-layer becomes the phellogen, and *Vahlia*, in which the epidermis does so.

Certain species of *Saxifraga*, namely those of the section *Euaizoonia*[1], and those named in the foot-note[2] belonging to two other sections, as well as the genus *Rodgersia* are characterized by the possession of medullary vascular bundles, the genus *Peltiphyllum* by the occurrence of medullary and cortical bundles[3].

Lastly, two or three cases of the occurrence of secretions in some of the plants belonging to the tribes under consideration may be referred to. According to Thouvenin, an intercellular system, filled with resinous contents, which are soluble in alcohol, is found in the cortex of *Vahlia capensis* and *Donatia magellanica*. Other kinds of secretory organs are found in *Parnassia palustris*,

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[1] The following have been investigated: *S. Aizoon*, *S. altissima*, Kern., *S. Andrewsii*, Harv., *S. Cotyledon*, *S. crustata*, *S. Hostii*, *S. lingulata*, *S. longifolia* and *S. mutata*.

[2] These are: *S. pensylvanica*, L. (section *Boraphila*); *S. hirsuta*, L., *S. umbrosa*, L., *S. serrata*, Sternb. (section *Robertsonia*).

[3] Schwendener's statements (Mech. Prinzip., 1874, p. 143) as to the occurrence of cortical vascular bundles in *Saxifraga ligulata* have been confirmed neither in *S. ligulata*, Wall. nor in *S. ligulata*, Murr. (= *S. sarmentosa*, L. f.).

namely secretory cells with wide lumina, in the pith, in the tissue of the xylem, and in the pericycle of the rhizome.

B. Philadelpheae, Hydrangeae, Escallonieae, Cunonieae and Ribesieae.

2 B. Structure of the Leaf[1]. In almost all the species the leaves have bifacial **structure**; according to Holle, leaves of approximately centric structure occur in *Bauera* only. The palisade-tissue frequently consists of one layer, but occasionally of more. The genera *Deutzia*, *Abrophyllum* and *Argophyllum*, as well as most species of *Philadelphus*, for example, are characterized by a one-layered palisade-tissue (Holle). Spicular cells in the mesophyll ('faisceaux de cellules scléreuses au milieu du parenchyme lacuneux') are only known in *Pancheria Vieillardi* (Thouvenin).

The **epidermal cells** of the leaf have straight or undulated lateral walls.

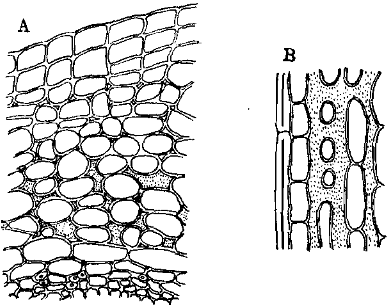

Fig. 67. *Vahlia capensis.* A, Transverse section through the cortical tissue of the axis. B, Longitudinal section through the same.—After Thouvenin.

A special marking of the cuticle has not been observed; distinct formation of papillae has not been met with. The epidermal cells are usually low in a transverse section of the leaf; they are elongated like a palisade, especially in *Codia montana*, Forst., in less degree in *Abrophyllum ornans*, Hook. f. and *Weinmannia trichosperma*, Cav. The development of a 1–3-layered hypoderm on the upper side of the leaf is a very widespread phenomenon. Holle describes it in *Hydrangea integerrima*, Engl., *H. peruviana*, Moric.; *Pileostegia viburnoides*, Hook. f. et Th.; *Broussaisia pellucida*, Gaud.; *Escallonia florida*, Poepp. et Endl., *E. littoralis*, Phil., *E. leucantha*, Remy, *E. macrantha*, Hook. et Arn., *E. rosea*, Phil.; *Polyosma integrifolia*, Bl. (locally), *P. serrulata*, Bl.;

[1] Most important literature: Holle and Thouvenin, ll. cc.; the researches of these authors extend to the following genera, which are enumerated in the serial order of Engler's system of classification: tribe Philadelpheae: *Carpenteria*, *Philadelphus*, *Jamesia*, *Fendlera*, *Deutzia*, *Whipplea*; tribe Hydrangeae: *Deinanthe*, *Cardiandra*, *Platycrater*, *Hydrangea* (incl. *Cornidia*), *Schizophragma*, *Pileostegia*, *Dichroa*, *Broussaisia*, *Decumaria*; tribe Escallonieae: *Brexia*, *Roussea*, *Anopterus*, *Abrophyllum*, *Itea*, *Quintinia*, *Escallonia*, *Forgesia*, *Polyosma*, *Argophyllum*, *Carpodetus*, *Phyllonoma*; tribe Ribesieae: *Ribes*; tribe Bauereae: *Bauera*; tribe Cunonieae: *Belangera*, *Caldcluvia*, *Platylophus*, *Ceratopetalum*, *Anodopetalum*, *Cunonia*, *Weinmannia*, *Pancheria*, *Callicoma*, *Codia*.

Carpodetus serratus, Forst. (locally); *Roussea simplex*, Smith; *Argophyllum nitidum*, Forst.; *Platylophus trifoliatus*, Don; *Codia montana*, Forst. (resembling stone-cells); *Cunonia capensis*, L.; *Anodopetalum biglandulosum*, A. Cunn.; *Weinmannia australis*, Cunn., *W. Hildebrandtii*, Baill., *W. trichosperma*, Cav.; *Callicoma Stutzeri*, F. v. Müll. The epidermis is divided locally in *Carpenteria californica* (Thouvenin). Epidermal and hypodermal cells with mucilaginous inner membrane have been met with only in the tribe Cunonieae, where they have been found in all the genera investigated.

The **stomata** are found exclusively on the lower side of the leaf. In the majority of the genera and species they are surrounded by a considerable number of neighbouring cells, which, at any rate in the mature leaf, exhibit no special arrangement, and are occasionally distinguished by their smaller size from the remaining epidermal cells. Subsidiary cells parallel to the pore have been met with only in *Dichroa febrifuga*, Lour., in the genus *Quintinia*, and in certain groups of very closely allied species of the genus *Hydrangea*. The guard-cells usually lie in the plane of the epidermis.

According to Holle, species of *Itea*, *Roussea*, *Abrophyllum*, *Argophyllum*, *Quintinia*, *Cunonia*, *Platylophus* and *Ribes* are characterized by the possession of fairly small pairs of guard-cells of nearly circular outline. *Bauera*, *Belangera* and some species of *Escallonia* exhibit ridge-like lumps on the guard-cells, appearing like small horns in a transverse section of the leaf. The species of *Brexia* are characterized by a kind of double front-cavity, inasmuch as the lower portion of the cavity has an elliptical shape when seen from the surface, but widens out above to such an extent that it attains a circular outline in surface-view.

In the tribes which we are considering, the vascular bundles of the smaller **veins** are either vertically transcurrent or embedded. Occasionally both structural features occur within the same genus, e.g. in *Callicoma*; for details see Holle, whose statements, however, require further critical examination.

Oxalate of lime is excreted in very various forms, namely as clustered crystals, ordinary solitary crystals, styloid-like crystals, raphides, small acicular crystals, and crystal-sand. The following statements refer to the mode of excretion in the different tribes.

Throughout the tribe Hydrangeae raphide-sacs filled with mucilage occur. In the leaf they mostly lie in the middle of the mesophyll and parallel to the surface of the leaf, more rarely in the palisade-tissue, and in that case they follow the direction of the palisade-cells; the raphide-sacs of the palisade-tissue occasionally (*Decumaria*) give rise to transparent dots. In the axis the raphide-sacs occur in the pith, bast and primary cortex. In the cortex of *Schizophragma hydrangoides*, S. et Z. and *Pileostegia viburnoides*, Hook. f. et Th. in addition to raphide-sacs peculiar crystal-sacs occur, which are filled with small acicular crystals and mucilage and are to be regarded as a modification of the ordinary raphide-sacs; and further, in the axis and leaf of *Cornidia*, 'styloid-like and clinorhombic' crystals are found (Holle).—According to Holle and Thouvenin, in the tribe Philadelpheae, the two closely related genera *Philadelphus* and *Carpenteria* alone possess clustered crystals.—Among the Escallonieae, according to Holle, *Anopterus*, *Itea*, *Escallonia*, *Forgesia*, *Polyosma*, *Carpodetus* contain clustered crystals in the leaf and axis, while *Quintinia*, *Brexia* and *Roussea* have ordinary solitary crystals also. With regard to *Escallonia*, however, it may be added, that in *E. Sellowiana*, DC. and *E. montevidensis*, DC. styloids also have been found in the bast (Möller, Solereder). In *Argophyllum* oxalate of lime has not been observed; in *Abrophyllum* it occurs in the form of finely granular crystal-sand in cells of the cortex, pith and spongy parenchyma.—In the Cunonieae Holle states that, as a rule, ordinary solitary and clustered crystals occur; in *Bauera* we find solitary crystals only, in the species of *Ribes* clustered crystals only, and in a transverse section of the branch they are arranged in concentric rings in the bast, in the same way as in the bark of the pomegranate.

Amongst internal **secretory organs** the occurrence of mucilage-cells in the cortex of *Weinmannia trichosperma*, Cav. corresponds to the mucilaginous

cells already described in the epidermis of the leaf. Further, in *Abrophyllum ornans*, Hook. f., there is a ring of laticiferous sacs (Holle) in the pericycle. They are parenchymatous cells, which are elongated in the vertical direction, and are arranged in rows; the only essential distinction from the surrounding cells lies in their whitish and friable contents, which are insoluble in alcohol, and soluble in chloroform. Lastly, narrow intercellular spaces, resembling canals, which are filled with resin, and exhibit a similar differentiation to those of *Donatia* and *Vahlia* (see p. 313), have been met with by Thouvenin in *Roussea simplex*, in the tissue of the pith and primary cortex, and in the median vein of the leaf, above and below the vascular bundle-system.

The **hairy covering** consists of clothing and glandular hairs. The simplest

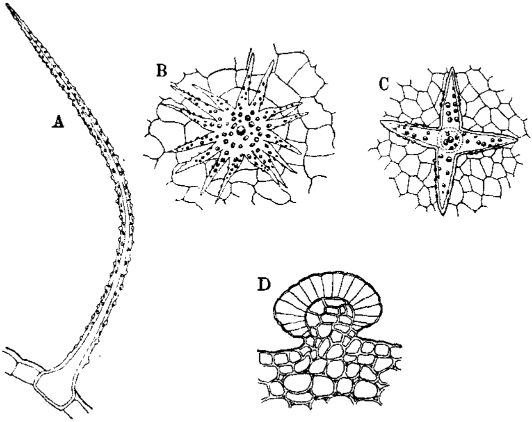

FIG. 68. A, Simple trichome of *Philadelphus Billiardi*, Köhne. B, Stellate hair from the upper side of the leaf of *Deutzia pulchra*, Vidal. C, Stellate hair from the upper side of the leaf of *Deutzia gracilis*, Sieb. et Zucc. D, Stem-gland of *Escallonia viscosa*.—A–C Original, D after Thouvenin.

type of the former is represented by ordinary unicellular hairs of varied length. In the Philadelpheae (Fig. 68, *A*) and Hydrangeae their walls are very frequently provided with small knobs, and are always, although occasionally only slightly, incrusted with carbonate of lime. The unicellular trichomes of the Cunonieae, Escallonieae and species of *Ribes*, on the other hand, are not calcified. By the association of simple unicellular hairs, tufted hairs arise, which occur in *Broussaisia*, *Callicoma*, *Cornidia* and *Pileostegia*, and only possess calcified walls in the last two genera. Unicellular one-armed hairs have been met with in *Abrophyllum*, two-armed trichomes in *Argophyllum*, *Deinanthe* and, according to Engler, in *Colmeiroa*. The malpighian hairs of *Argophyllum* and *Deinanthe* have a multicellular stalk; the wall of the latter is calcified only in *Deinanthe*. Finally, we may mention the unicellular stellate hairs (Fig. 68, *B–C*), characteristic of the genus *Deutzia*; they have pointed

arms, all spread out in the same plane, and a verrucose surface; the walls of these hairs are silicified (Mohl and Wicke) and also calcified; the number of the arms differs in the individual species.

External glands have only been observed on the leaves of the genera *Abrophyllum*, *Escallonia*, *Quintinia* and *Ribes*. The external glands of *Escallonia* (Fig. 68, *D*), which also occur on the stem, and occasionally give rise to 'varnished' leaves, are glandular shaggy hairs with a multiseriate stalk of variable length, and a spherical or peltate head, the centre of which is occupied by isodiametric cells, while the epidermal cells are elongated like a palisade. The glands on the leaf and stipules of *Ribes* exhibit a similar structure. In *Abrophyllum* the leaf bears small glandular hairs, with a sunk stalk of few cells and a unicellular head; in *Quintinia*, multicellular peltate glands occur on the leaf. External glands also occur on the stipules of *Cunonia* (Hanstein) and *Ceratopetalum* (Thouvenin) in the form of glandular shaggy hairs similarly constituted to those of *Escallonia*.

Occasionally the leaf-teeth also have a glandular function, e.g. in species of *Ribes*, *Decumaria*, *Deutzia*, *Philadelphus*, *Escallonia* and *Cunonia*, according to Reinke. With regard to their structure the glandular apparatus in *Cunonia* is formed by glandular shaggy hairs with a palisade-like epidermis, and in *Escallonia* by the tips of leaf-teeth having an analogous structure; in both cases the gland exudes a resinous excretion. In the remaining cases the termination of a vascular bundle, provided with an epithema containing mucilage, passes into the leaf-tooth, and the epidermis clothing it includes one or few water-pores.

It may be noted here that cork-warts have been observed on the leaves of *Cornidia* and of *Roussea simplex*; these must not be confounded with glands. The spines of the species of *Ribes* are, according to Delbrouck, essentially periblem-structures.

With regard to the structure of the **petiole**, which has been investigated by Thouvenin and Petit, it is sufficient to mention that, in all investigated Cunonieae, Philadelpheae, Ribesieae, and most Escallonieae (incl. Brexieae), three vascular bundles pass into the petiole, in *Escallonia* and *Phyllonoma ruscifolium* on the other hand, only one vascular bundle; as to their further course, which in the Cunonieae, for example, is constant throughout, see the literature cited.

3 B. Structure of the Axis. Regarding the structure of the **wood**, the following summary, which takes account of Holle's statements, may be given. The medullary rays vary in breadth. In the Philadelpheae, Hydrangeae and Escallonieae they are 1–3-seriate, not much broader in the Cunonieae, but reaching seven cells in breadth in *Ribes*. In a transverse section the vessels are usually isolated, and never have very wide lumina (maximum diameter = ·04 to ·06 mm.). A quadrangular shape in transverse section is characteristic of the lumen of the vessels in the Philadelpheae and Hydrangeae. The perforations of the vessels are either exclusively scalariform or both scalariform and simple in the same species. The number of bars in the scalariform perforations varies, and is often very considerable (see Holle and Solereder).

Holle describes exclusively scalariform perforations in *Philadelphus*, *Jamesia*, *Fendlera*; *Deinanthe*, *Platycrater*, *Hydrangea* (with *Cornidia*), *Schizophragma*, *Pileostegia*, *Dichroa*, *Broussaisia*, *Decumaria*; *Roussea*, *Abrophyllum*, *Itea*, *Quintinia*, *Escallonia*, *Polyosma*, *Forgesia*, *Agrophyllum*; *Ribes*; *Caldcluvia*, *Platylophus*, *Anodopetalum*, *Cunonia*, *Weinmannia*, *Callicoma*, *Codia*;—simple and scalariform perforations side by side in *Bauera*, *Belangera*, *Brexia*, *Cardiandra*, *Ceratopetalum* and *Whipplea*; in these genera the scalariform perforations usually (except in *Bauera*) predominate.

According to the statements in my 'Holzstruktur,' the wall of the vessel where it is in contact with the parenchyma of the medullary rays either bears bordered pits only (*Philadelphus*, *Itea*, *Escallonia*, *Ribes*) or large simple pits

as well (*Cunonia, Callicoma* [1]). The wood-parenchyma is not abundantly developed; chambered parenchyma, containing crystals, occurs for example in *Cunonia capensis*, L. and *Callicoma Stutzeri*, F. v. Müll. According to my observations, the wood-prosenchyma, which mostly has thick walls, either bears bordered pits exclusively (*Philadelphus, Cunonia, Callicoma, Escallonia* and *Itea*), or bordered and simple pits (*Deutzia, Ribes*), or simple pits only (*Hydrangea*). The wall of the prosenchyma with bordered pits in *Philadelphus coronarius*, L., is provided with a spiral band; the lumen of the simple-pitted wood-fibres in *Deutzia* and *Ribes* is septate.

Holle's statements regarding the pitting of the wood-prosenchyma may be quoted as follows, but they need further critical examination. According to Holle the following genera have wood-prosenchyma with bordered pits: *Jamesia, Philadelphus, Whipplea; Deinanthe, Broussaisia; Brexia, Roussea, Anopterus, Abrophyllum, Itea, Quintinia, Escallonia, Forgesia, Polyosma, Argophyllum, Carpodetus; Caldcluvia, Platylophus, Ceratopetalum, Anodopetalum, Cunonia, Weinmannia, Pancheria, Callicoma*;—the following have prosenchyma with simple pits: *Cardiandra, Hydrangea, Platycrater, Dichroa, Bauera, Belangera*;—while the following have prosenchyma with simple and bordered pits: *Deutzia, Schizophragma, Pileostegia, Decumaria* and *Ribes*.

The **pith** has been little investigated. According to Mentovich, it is heterogeneous in *Deutzia* and *Hydrangea*. In *Deutzia* the central part of the pith subsequently collapses, and the stem consequently becomes fistular.

As regards the structure of the cortex, the cork principally requires discussion. According to the concordant statements of different authors, amongst whom Holle has examined the most abundant material, superficial development of cork, originating in the epidermis or in the subepidermal cell-layer, is characteristic of the Bauereae, Cunonieae and Escallonieae (exclusive of *Escallonia*); while internal (pericyclic) origin of the cork is characteristic of the Philadelpheae, Hydrangeae, *Ribes* and *Escallonia*. According to Holle, the superficially formed cork, as a rule, consists of plate-like radially compressed cells, while the pericyclic cork is composed of cells which have relatively wide lumina, and are frequently elongated in the radial direction. In *Philadelphus, Jamesia, Anodopetalum* and *Whipplea* the cork exhibits a remarkable differentiation. In the two first-named genera, rows of cork-cells, which are elongated in the radial direction, alternate with others, which are compressed in the same direction; the latter are sclerotic in *Philadelphus*. *Anodopetalum* possesses lamellated cork ('Lamellenkork'). In this genus the epidermis and the subjacent cell-layers of the primary cortex successively give rise to phellogen, from without inwards, and each produces a cork-lamella, consisting of a few layers of cells. Lastly, some of the cork-cells of *Whipplea* are sclerosed in the form of a horse-shoe, as seen in a transverse section of the branch; in this case the sclerosis extends to the inner tangential wall and the contiguous radial walls. Phelloderm-formation occurs; the ring of stone-cells situated on the inner side of the cork-cambium in *Broussaisia, Cornidia, Decumaria, Pileostegia* and *Schizophragma* is without doubt of the nature of a phelloderm.

The outer portion of the primary cortex is frequently collenchymatous. Groups of stone-cells have been observed in the primary cortex of *Roussea simplex*, Sm., slightly thickened sclerenchymatous cells in that of *Quintinia Sieberi*. The nature of the pericycle varies. In species of *Deutzia, Philadelphus, Hydrangea* and *Ribes* no sclerenchyma is present in the pericycle;

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[1] Holle states that large simple pits occur on these parts of the vessel-wall in some cases, viz. in the Cunonieae and in *Broussaisia*; he describes small indistinctly bordered pits in the Hydrangeae, but everywhere else distinct bordered pits.

in *Anopterus* and *Itea*, on the other hand, the pericycle contains isolated groups of bast-fibres, in *Phyllonoma* a ring of bast-fibres, in *Polyosma* a ring of stone-cells, and in the Cunonieae, *Quintinia* and *Abrophyllum* a composite and continuous sclerenchyma-ring. Secondary hard bast is not commonly developed; it has been observed by Möller and Thouvenin in species of *Weinmannia, Cunonia, Geissois, Pancheria* and *Callicoma*.

C. The Anomalous Genus Cephalotus.

The genus *Cephalotus*, which is appended to the Saxifragaceae as a 'genus anomalum' by Bentham and Hooker, is characterized by the well-known ascidiform leaves. The following points, quoted chiefly from Goebel, may be mentioned respecting their structure.

The epidermis on the outer side of the lid of the pitcher consists of flat cells with undulated lateral walls. Amongst the epidermal cells depressed glands occur, the structure of which recalls that of the glands of *Sarracenia*. Thus, in surface-view, they exhibit two inner triangular cells, touching one another along one side, and these are surrounded by four other symmetrically arranged cells; two further cells adjoin these six cells internally. The lower side of the lid is differentiated as a slippery surface, and so are the folds of the collar.

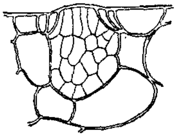

Fig. 69. Gland of *Cephalotus*.—After Goebel.

Three regions may be distinguished on the inner surface of the pitcher. The portion lying below the collar contains numerous glands (Fig. 69), which scarcely project above the surface of the wall of the pitcher, and are delimited towards the surrounding tissue by a suberized membrane. The glands of this zone are roughly flask-shaped, and consist of a large ventral part, formed by irregularly polygonal cells, and of a fairly broad neck-portion, composed of a layer of palisade-like cells, elongated at right angles to the surface of the pitcher. On the two lateral, brightly-coloured projections, which penetrate like cushions into the interior of the pitcher, specially large glands are found, as well as numerous water-pores, which, according to Goebel, are peculiar, inasmuch as the subjacent parenchyma-cell, which is rich in contents, protrudes through the widely open pore. The lowest portion of the inner wall of the pitcher consists of epidermal cells with undulated boundaries, and without glands.

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CRASSULACEAE.

1. Review of the Anatomical Features. The stomatal apparatus is characteristic of most members of the Order, the pair of guard-cells being surrounded by a simple or multiple girdle of three subsidiary cells. In addition to the air-pores (stomata), water-pores occur in many cases. A hairy covering is rare, but curiously-shaped bladders (*Rochea*) and glandular hairs have been observed. Oxalate of lime is excreted in the form of ordinary solitary crystals, sphaerites and crystal-sand; the latter either occupies the lumen (*Cotyledon*, *Sedum*), or is embedded in the membrane (*Crassula*, *Rochea*, *Sempervivum*) of the cell. Tannin is frequently present in the Order, and is occasionally stored up in special cells, which are distinguished either by their small size or by their development as long sacs; in the leaf the latter are found, especially in the epidermis or in the subepidermal layer of cells. As regards the structure of the axis, the secondary vessels, which are always enclosed in unlignified tissue, have simple perforations and simple-pitted walls; the wood-prosenchyma bears simple pits. The appearance of the xylem in transverse section varies, inasmuch as the thin-walled groups of tissue, together with the secondary vessels and the wood-prosenchyma, may or may not be present, and inasmuch as both may be concerned to a varying extent in the formation of the xylem. Medullary rays are rarely developed. Where cork occurs, its formation takes place in a superficial layer of cells. The following features also require special mention: the occurrence of cortical vascular bundles in species of *Rochea*, *Sedum* and *Sempervivum*, the remarkable stem-structure of *Sedum populifolium*, Pall., and the anomalous root-structure of *Sedum maximum*, Sut.

2. Structure of the Leaf. The **leaf-structure** is, as a rule, centric or intermediate between bifacial and centric in structure. Typical palisade-tissue is only rarely present.

As a rule the **stomata** occur on both sides of the leaf. They are usually surrounded by subsidiary cells, exhibiting a characteristic arrangement (Fig. 70, *A*). For the stomata arise by divisions, resembling those of an apical cell; by successive walls, arranged in three directions, as seen in surface-view, the initial cell becomes divided into a girdle of subsidiary cells (mostly multiple) which encircles the mother-cell of the guard-cells. An exception is afforded by *Tillaea muscosa*, in which the pair of guard-cells is surrounded by 3–5 ordinary epidermal cells (Benecke). In many cases (species of *Bryophyllum*, *Crassula*, *Kalanchoe*, *Rochea*, *Sedum*, *Umbilicus*), water-pores occur in addition to the air-pores. These water-pores give rise to small pits or spots on the leaf, which are frequently visible even with the naked eye, and were first pointed out by Treviranus; they were subsequently investigated in detail by Magnus, De Bary, Mori and Berge. Pits or spots of this kind, containing water-pores, are either to be found distributed over both surfaces of the leaf (e.g. in *Crassula portulacea*, Lam.), or scattered over the upper side

only (e. g. in *C. cordata*, Ait.), or merely forming a row immediately within the margin of the leaf; in the latter case they either occur on both surfaces (e.g. in *C. lactea*, Ait.) or only on the lower surface of the leaf (e. g. in *C. lycopodioides*, Lam.). The epidermis in these areas usually consists of small cells with delicate walls, amongst which stomata with short pores and of smaller size than the air-stomata of the same leaf are situated, mostly several in each area (5 or 6, in *Crassula lactea* as many as 25); in *Crassula perforata* and *Rochea coccinea* the whole pit is formed by a single water-pore, which is, however, of large size, and somewhat depressed. Below the epidermis of these small pits and spots the termination of a vascular bundle, provided with a small-celled epithema, is found.

In the Crassulaceae, as in other succulent plants, the excretion of wax on the **epidermis** is not an uncommon phenomenon. Thus the leaves of *Sempervivum glaucum*, *S. tectorum* and *S. calcareum*, for example, have a distinct waxy glaze, which is uneven (finely verrucose) in the first-named species; in *Cotyledon orbiculata*, L., the thin waxy glaze of the leaves is provided with

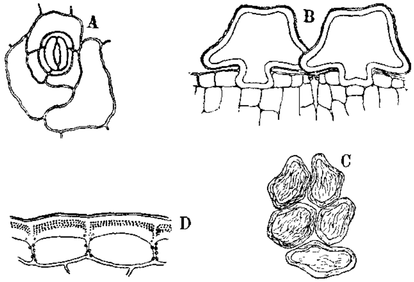

FIG. 70. A, Type of stoma in *Sedum spurium*. B, C, Bladder-like epidermal cells of *Rochea falcata*, DC. D, Transverse section through the epidermis of the anterior portion of the leaf of *Sempervivum calcareum*, Jord.— A after Strasburger, B, C after Areschoug, D after Solms-Laubach.

numerous upright and convergent prolongations in the form of small rods, 10 μ in height, and nearly 1 μ in thickness (De Bary).

The formation of **hairs** is not common in the Order. In the first place, very peculiar trichomes, which may be described as bladders, have been observed in some of the species of the genus *Rochea*, e. g. *R. falcata* (Fig. 70, *B–C*). These bladders are special epidermal cells with thick walls, the fairly broad base of which is inserted among the ordinary cells of the epidermis, whilst above the level of the latter they become enlarged to such an extent as to cover up the neighbouring epidermal cells. In *R. falcata* they are distributed over the whole surface of the leaf; in *R. coccinea* they are restricted to the margin. Besides these bladders external glands also occur. Wagner mentions capitate glandular hairs in *Cotyledon*, *Aeonium* and *Echeveria*; Mori describes shortly stalked, capitate glandular hairs composed of few cells on the axis and leaf of *Sempervivum glutinosum*, where they secrete a considerable amount of mucilage, which covers these organs. I have myself occasionally met with glandular hairs, having an elongated biseriate stalk and a spherical multicellular head in *Sempervivum Smithii*, Sims.

According to Schönland, **oxalate of lime** is present in large quantity,

and is excreted in the form of solitary crystals, sphaerites and crystal-sand. Cells filled with crystal-sand have been observed by me in the pith and cortex of *Cotyledon teretifolia*, Thunb., and *Sedum spurium*, Bieb., and by De Bary in *Sedum ternatum*. Crystal-sand, moreover, also occurs as a deposit in the cell-membrane (Fig. 70, *D*). Thus, according to Solms-Laubach, small crystals of oxalate of lime (curiously enough, without action on polarized light) are found in the cellulose-layer of the outer wall of the epidermal cells in the leaf of *Sempervivum calcareum*, Jord.; further, according to my own observation, small crystals also occur in the thin or somewhat collenchymatous membranes of the cells of the pith and primary cortex in *Rochea coccinea*, DC., and in the membranes of the cells of the primary cortex in *Crassula scabra*, L.

The Crassulaceae are also rich in **tannin**. In the leaf, according to Wagner, it occurs especially in the veins, where it is found in the parenchyma of the bundles and in the sheath of the latter, but it is also present in the mesophyll. Generally the tannin-cells are not essentially distinguished from the cells surrounding them. The reverse is more rarely the case; the tannin-containing cells are then either smaller than the others, or they are differentiated as sacs of more or less considerable dimensions.

The former is, for example, the case in the epidermis of the stem of *Aeonium glutinosum* and *Sedum Aizoon*, in the middle and inner zones of the cortical parenchyma of *Aeonium Saundersii*, in the subepidermal tissue of the leaf of *Aeonium Saundersii* and *A. glutinosum*, and in the internal leaf-tissue of *Crassula spathulata* and *Echeveria coccinea*. Tannin-sacs, on the other hand, have been observed by Engler in the epidermis of the leaf in *Sedum spurium*, by Wagner in the epidermis or subepidermal layer of the leaf in *Aeonium barbatum*, *A. Castello-Paivae*, *Sempervivum holochrysum*, *S. pulchellum*, *Sedum hybridum*, *S. purpureum* and *S. Ewersii*, by Höhnel in the subepidermal cell-layer of the leaf in *Aeonium decorum*, and (according to my own observation) in the same position in *Sempervivum Smithii*, Sims., and lastly by Strasburger in the pericycle of the stem of *Sedum maximum*. The brown-spotted appearance of the dried leaves of *Sempervivum Smithii*, for example, is due to these tannin-sacs. Occasionally the walls of the tannin-sacs are more strongly thickened or (e. g. in *Aeonium barbatum* and *Sempervivum pulchellum*) suberized.

3. Structure of the Axis. The outer **cortex** is usually fleshy and strongly developed. It either consists of succulent parenchyma only, or its outer portion also contains weakly developed collenchyma. In *Bryophyllum* and *Sedum* the cork is developed in the epidermis; in other cases, according to Schönland, the snbepidermal cell-layer or a deeper layer of the primary cortex becomes the phellogen.

As regards the **fibro-vascular system**[1], it may be noted that hard bast has not been observed in any member of the Order, and that the phloem is only slightly developed. Sieve-tubes are present it is true, but, as is generally the case in succulent plants, they have narrow lumina, and are consequently not easily demonstrated. With respect to the differentiation of the xylem, the following types may be distinguished in those species with a well-developed axis. In a first series of species the xylem-mass, apart from the primary groups of vessels, consists of a closed ring of wood, situated on the outer side of the primary vessels, and composed of prosenchyma only; it contains neither vessels nor medullary rays. This is the case in *Umbilicus pendulinus* and *Crassula rubens*, according to Régnault; in *Sedum acre*, *S. rupestre* and *S. stellatum*, according to Mori; in *Sedum spurium*, Bieb., according to Koch and my own investigations, and contrary to Mori's statement; in *Sedum album*, L. and *S. reflexum*, L., according to Schönland and Koch. The second

[1] The fibro-vascular system is very much reduced in the aquatic type *Tillaea aquatica*, L. (for which see Caspary, loc. cit.).

type is distinguished from the first by the fact that small groups of vessels, accompanied by elongated and unlignified parenchyma, appear in the ring of fibres. To this type belong, according to De Bary, *Sedum maximum* and *S. populifolium*, as well as *Echeveria pubescens*, and according to Schönland, *Sedum Aizoon*, L., *S. deltoideum*, Ten., *Sempervivum Haworthii*, Hort. Angl., *Crassula falcata*, Willd. and *Bryophyllum*. If we now imagine the groups composed of the vessels and the accompanying unlignified tissue to be larger and arranged in concentric circles, we obtain the appearance of the transverse section of *Echeveria* sp., according to Schleiden, of *Rochea falcata*, *Sempervivum arboreum*, *S. Haworthii* and *S. 'leucoblepharum,'* according to Régnault, and of *Cotyledon teretifolia*, Thunb., *Crassula scabra*, L., *Kalanchoe grandiflora*, Wall. and *Rochea coccinea*, DC., according to my own investigations. A slight further modification of the type just described is brought about when the xylem-mass shows an alternation of continuous bands of libriform and of vessels, as in *Sedum altissimum* and *S. dasyphyllum* according to Mori. The stem-structure of *Crassula portulacea* and of *Sedum oxypetalum* must be considered as representing a special type. In these plants the chief mass of the xylem, according to Régnault, consists of unlignified tissue, in which vessels are distributed in an irregular manner; wood-fibres are absent. In these species also primary medullary rays occur, and separate the vascular bundles from one another.

At this point the interesting and complicated structure, found in the older stems of *Sedum populifolium* and described by Koch and Strasburger, may be referred to. The young stem of this species (see above), externally to the primary groups of vessels, contains a ring of wood-fibres, enclosing isolated vessels only. Subsequently the cambium produces, in the first place, a ring of thin-walled tissue with groups of vessels, which lie on the same radii as the primary vessels; but this is followed by a second ring of fibres, which only differs from the first in having more numerous groups of vessels embedded in thin-walled tissue, and so on. The ring of thin-walled tissue, which succeeds the first ring of fibres, soon becomes filled with contents, and assumes the appearance of a pith; its innermost layer of cells develops into a cork-cambium, and the cork-tissue derived from the latter shuts off all the tissue lying internally to it (pith, primary groups of vessels and the first ring of fibres) from the outer woody tissue. The phenomena described are repeated. In each period of vegetation a new ring of wood is developed, and begins with a zone of thin-walled tissue; and similarly in the innermost cell-layer of these zones successive layers of cork are formed.

The prosenchyma which occurs in the wood of the Crassulaceae has lumina of varied width, and is characterized by simple pits. The vessels of the secondary wood always bear simple pits or reticulate thickening, never bordered pits; their perforations are simple.

It remains to mention that concentric vascular bundles with central xylem have been observed in the cortex of some species; e.g. by Cornu in certain species of *Sempervivum*, belonging to the section *Aeonium* (*S. canariense*, *S. ciliatum*, *S. 'giganteum,' S. urbicum*), and in '*Greenovia terrae,*' by Schönland in *Sedum Rhodiola*, DC., and by Mori in *Rochea coccinea*, *R. falcata*, and *R. perfoliata*. They are occasionally developed in large numbers (up to 100).

NOTE.—Anomalous **root-structure** has been demonstrated in the mature napiform roots of *Sedum maximum*, Sut. and its allies. It occurs only in the middle (not in the upper and lower) portion of the roots. In transverse section this region shows a circle of concentric vascular bundles with central wood. Originally the fibro-vascular system of the roots possesses normal structure, as Koch was the first to show. Subsequently, however, the ring of cambium breaks up into a number of separate arcs, which extend round portions of the original xylem and enclose them in an annular manner.

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DROSERACEAE.

The anatomy of this Order, which consists of the genera *Drosera*, *Drosophyllum*, *Aldrovanda*, *Dionaea*, *Roridula* and *Byblis*, and is extremely interesting from the biological point of view, will only be discussed in broad outline. Only the first four of the above genera have been investigated in detail.

Glands of a certain characteristic structure (Fig. 71) are peculiar to all the members of the Order. They consist of a stalk of varied length and varied structure, and of a glandular head, which is composed of two layers of glandular cells and, beneath the latter, of a layer of suberized cells, called the middle layer; it is impossible to enter into details here regarding the physiology of the mucilaginous product of secretion.

The glandular tentacles occurring in the genera *Drosera*, *Drosophyllum*, *Roridula* and *Byblis* may be described as the most highly developed form of the glands in question; they have been more thoroughly investigated in the first two genera. The tentacles of *Drosera* (Fig. 71, *E*), which are situated on the surface of the leaf, consist of a multiseriate stalk, traversed by a strand of tracheides, and enlarged at the apex into an ellipsoidal glandular head. The innermost portion of the latter contains a strongly developed group of tracheides, which represents the termination of the strand of tracheides found in the stalk. This group of tracheides is adjoined by a bell-shaped simple layer (middle layer) of suberized and mostly elongated cells, which is directly superposed upon the group of tracheides both above and at the sides, whilst the margin of the 'bell' terminates in the outer surface of the epidermis. Still further outwards the two layers of glandular cells follow; they have delicate walls, and are distinguished in the fresh condition by red contents. The marginal tentacles of the leaf of *Drosera* are only a modification of those just described. In this case the glandular head has the form of a spoon, and possesses the three characteristic cell-layers of the gland on the concave upper side only, while the margin and the lower side consist of but one layer of cells; there is a group of tracheides below the three cell-layers of the upper side. The glandular tentacles of *Drosophyllum lusitanicum* (Fig. 71, *A*), which are mostly situated on the lower side of the leaf, may be easily referred to the same type as the glands found on the leaf-surface of *Drosera*. The only distinction lies in the fact that the glandular head (ultimately becoming filled with red contents, and forming the termina-

tion of the stalk of the tentacle, which here also is traversed by a strand of tracheides) is represented by a disc, slightly convex on its upper side; with this feature the smaller development of the group of tracheides, situated below the middle layer, is connected. A transition to the glands of those genera (*Dionaea*, *Aldrovanda*), which do not possess tentacles, is afforded by the sessile glands (Fig. 71, *B*), occurring scattered on the upper, and densely crowded on the lower side of the leaf in *Drosophyllum lusitanicum*. Apart from the absence of a stalk and of red contents, they have, on the whole, the same structure as the tentacular glands of *Drosophyllum*; the head, however, has a more flattened discoid shape, and only a small group of tracheides—in connexion with a branch of a vascular bundle of the leaf—is found below the middle layer. A step further takes us to the glands of the

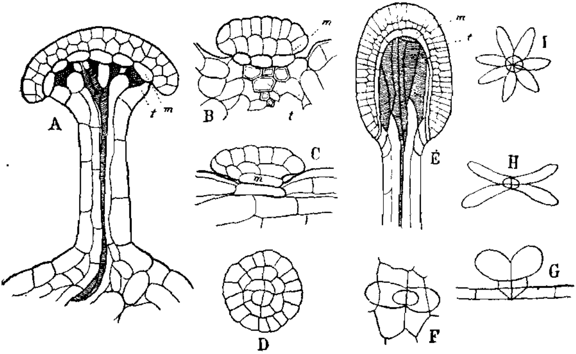

FIG. 71. A, Longitudinal section through a glandular tentacle of *Drosophyllum lusitanicum*; B, a similar section through a shortly stalked gland of *Drosophyllum*. C, Longitudinal section through the glandular disc of *Dionaea muscipula*; D, surface-view of the same gland. E, Longitudinal section through a glandular tentacle from the upper side of the leaf of *Drosera rotundifolia*. F, Two-armed hair of *Aldrovanda vesiculosa*. G, Glandular hair of *Drosera rotundifolia*. H, Four-rayed hair of *Aldrovanda*. J, Stellate hair of *Dionaea*. (*m*=middle layer, *t*=tracheides.)—A–C after Goebel, D and J after Fraustadt, E after De Bary, F and H after Caspary, G after Nitschke.

genus *Dionaea* (Fig. 71, *C–D*), which has no tentacles; its glands are present only on the upper side of the leaf, and in strongly growing plants are filled with a beautiful purple-red fluid. The two-layered glandular disc is very similar to that of the short-stalked glands of *Drosophyllum*; the cuticularized middle layer consists of only two cells, and so does the stalk, which is situated in the same plane as the epidermal cells of the leaf; tracheides are completely absent below the middle layer, and hence there is no connexion with the network of veins in the leaf. In surface-view (Fig. 71, *D*) the glandular disc shows three circles of polygonal cells; the innermost circle is, as a rule, composed of four cells, the middle one of eight, the outermost of sixteen. It may here be noted that glands, having an analogous structure to those of *Dionaea*, but sometimes with a still smaller head, and a correspondingly smaller number of glandular cells, are frequently also met with in species which possess tentacles, e.g. in *Drosera binata*, Labill. and *D. spathulata*,

Labill. The glands of *Aldrovanda*, which are situated on the upper side of the middle, thicker part of the lamina, also approximate in structure to those of *Dionaea*. Here the number of glandular cells in both layers has become smaller; in surface-view the glandular disc appears to be formed by two circles of four and of eight cells respectively; in this case likewise tracheides are not present below the gland.

In addition to the glands hitherto mentioned, which in part belong to the category of emergences, other types of **hair** occur in the Order. In the first place, hairs with quite a short stalk and (owing to vertical walls) a two- or four-celled head (Fig. 71, *G*) are found in *Drosera*. In *Aldrovanda*, shortly stalked, two-armed and four-armed (mucilage-excreting) hairs (Fig. 71, *F* and *H*) occur; the former, which are similar to malpighian hairs, but have the terminal portion (with equal arms) consisting of two cells, not one, occur on the petiole, on the lower side of the middle thick part of the lamina, on the bristles and on the stem; the latter have four unicellular arms arranged in the form of a cross (of this form ×), and are inserted on the inner side of the thinner marginal portion of the leaf. In *Dionaea* the lower side of the lamina bears almost sessile stellate hairs (Fig. 71, *J*), with four to nine, often eight ray-cells spread out in one plane. Other forms are (1) the simple hairs, which occur on the infolded leaf-margin of *Aldrovanda*, being long or short protrusions of the middle part of the outer wall of the marginal cells, and (2) the shaggy hairs, which occur in *Drosera*, and occasionally bear the above described capitate hairs, sometimes even terminating in a similar capitate hair.

To the description of these hairs I may add a short discussion of the marginal bristles of the leaf in *Dionaea*, of the sensitive bristles in *Dionaea* and *Aldrovanda*, and of the large bristles at the base of the leaves in *Aldrovanda*, which last may or may not be regarded as pinnate segments. The marginal bristles of *Dionaea* are emergences; they are covered on all sides with stomata and stellate hairs, and are traversed internally by a vascular bundle. The sensitive bristles of *Dionaea*, as is well known, usually occur three together on the inner side of each of the two halves of the leaf; vascular bundles do not pass into them; on the other hand, they are provided with a joint. The bristle-like shaggy hairs, which are found between the glands on the inner side of the middle part of the leaf of *Aldrovanda*, are homologous with the sensitive bristles of *Dionaea*; they are of simpler structure (consisting of tiers of two cells each), but are likewise provided with a joint. Lastly, the bristles (5–6 mm. long) at the base of the leaf of *Aldrovanda* consist of numerous rows of cells; all their cells contain chlorophyll, with the exception of the marginal cells, which are differentiated like teeth, and the three hairs at the end of the bristle.

With regard to the general **structure of the leaf**, it may be noted that the epidermis as a rule contains chlorophyll, that the mesophyll shows no differentiation into palisade and spongy tissue, and that the stomata have no special subsidiary cells. Oxalate of lime is present; detailed statements as to the form in which it occurs are wanting.

The following statements may be added regarding the detailed anatomical features of the leaf in the better-investigated genera, *Drosera*, *Drosophyllum*, *Aldrovanda* and *Dionaea*. In *Drosera rotundifolia* the mesophyll, according to Nitschke, consists of fairly uniform brick-like parenchyma; the epidermis contains chlorophyll; the stomata occur on both sides of the leaf. *Drosophyllum lusitanicum* likewise bears stomata on both sides of the leaf (Penzig). In *Dionaea muscipula* the chlorophyll-bearing epidermis is composed of quadrangular cells, which are elongated in the longitudinal direction of the leaf on the whole of the petiole and in the neighbourhood of the midrib of the lamina, whilst in the remaining part of the leaf they are elongated at right angles to this direction; the ground-tissue of the lamina consists

of elongated cells, which lie with their greater axis parallel to the midrib or the lateral veins; stomata occur only on the lower side of the lamina, but on both sides of the petiole (Fraustadt). In *Aldrovanda* (Caspary, H. Schenck), which represents an aquatic type, stomata are wanting, and the leaf is of very simple structure. A transverse section of the petiole shows polygonal, 5–6-angled cavities, below the chlorophyll-bearing epidermis; these cavities are separated from one another by parenchymatous lamellae, which are one cell broad and 3–4 cells deep; the centre of the petiole contains a single reduced vascular bundle, and the latter includes 1–3 annularly thickened cells at the base only. The middle, thicker portion of the lamina possesses a three-layered mesophyll. The thin marginal portion of the leaf of *Dionaea* has quite a peculiar structure; it appears to consist of a single layer of cells with slightly undulated lateral walls, between which smaller cells of elliptical outline are intercalated. As a matter of fact, however, the marginal portion must be regarded as consisting of two layers of cells. Of these two layers of cells the entire upper surface of the one (*A*) helps to form the upper side of the marginal portion of the leaf, whilst the entire lower surface of the other layer (*B*) contributes to the formation of the lower side of the marginal portion; in addition to this, however, the cells of the layer *A* take part in the formation of the lower side of the marginal portion of the leaf by means of several papillose prolongations of their lower cell-walls, which penetrate between the cells of the layer *B*, but do not project beyond the level of the latter cells; and conversely the cells of the layer *B* exhibit similar papillose prolongations, which take part in the formation of the upper side of the marginal portion. The apparent elliptical cells, previously referred to, thus merely represent the papillose projections in surface-view.

Little is known regarding the **stem-structure** of the Droseraceae. The stems of the submerged plant, *Aldrovanda vesiculosa*, have a very simple structure; the endodermis is wanting; the fibro-vascular system consists of a ring of phloem, and a little wood-parenchyma, the latter enclosing an air-passage, produced by the resorption of an axile group of eight or nine tracheae[1] with annular thickenings (H. Schenck). In the scapes of the Droseraceae (*Drosera*, *Drosophyllum*, *Byblis*, *Roridula*) Oels describes a sclerenchymatous cylinder, composed of cells resembling bast-fibres, and more or less directly adjoining the ring of vascular bundles. These bundles occasionally represent transitions from the collateral to the concentric type with central phloem. The structure of the wood in the woody species (*Roridula dentata*, L. and *Drosophyllum lusitanicum*, Link) has been investigated by me. In both genera the wood-prosenchyma has bordered pits. The perforations of the vessels, however, differ in character in the two genera. They are scalariform and provided with many bars in *Roridula*, simple and circular or elliptical in *Drosophyllum*. In a transverse section of the stem, *Roridula* shows uni- or bi-seriate medullary rays, and isolated vessels of medium diameter (up to ·06 mm.); the walls of the vessel are spirally thickened, and exhibit bordered pitting where they are in contact with the parenchyma of the medullary rays. In *Drosophyllum lusitanicum* I have observed small vascular bundles in the cortex, which are inversely orientated as regards xylem and phloem. Oels describes similar cortical bundles as occurring in the scape of *Drosophyllum*, where they stand in direct connexion with the vascular bundles of the glandular organs of the scape.

With regard to the structure of the **root** according to Oels, the unlignified main roots of many species of *Drosera* are anomalous in structure, in so far as their ground-tissue contains concentric vascular bundles with centrally placed phloem instead of the normal radially differentiated bundle-system; these bundles are either arranged in a simple or multiple ring (*D. intermedia*, Hayne, and *D. cuneifolia*, Thunb.), or irregularly (*D. binata*, Labill.). According to Oels, the strongly developed cortical parenchyma of *D. macrantha*, Endl.,

[1] True vessels are wanting in *Aldrovanda* (Caspary).

and *D. trinervia*, Spreng., is composed of peculiar spirally thickened cells with wide lumina. Lastly, the cortical parenchyma of the root of *Drosophyllum lusitanicum* contains inulin, according to Penzig.

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HAMAMELIDEAE.

1. Review of the Anatomical Features. This Order is well characterized from the anatomical point of view. In the structure of the axis we have the following excellent characters: the narrow medullary rays; the relatively small lumina of the vessels, which are mostly polygonal in transverse section, have exclusively scalariform perforations with many bars, and bear large simple pits, where they are in contact with the parenchyma of the medullary rays; the wood-prosenchyma, with typical bordered pits; the slight development of wood-parenchyma; the composite and for the most part completely continuous sclerenchymatous ring in the pericycle; as well as the superficial development of cork. The leaves are bifacial in structure in all the members of the Order, and have stomata on the lower side only, the stomata throughout being accompanied by two or more subsidiary cells, which are parallel to the pore. In most of the Hamamelidoideae [1] the hairy covering consists of tufted hairs; unicellular simple hairs occur in *Liquidambar*. Glandular hairs are absent. Oxalate of lime is excreted in the form of rhombohedral and clustered crystals. The Bucklandioideae [2] possess clustered crystals only, the Hamamelidoideae solitary crystals only in the ground-tissue of the leaf; the latter occasionally give rise to transparent dots. The Altingieae [2] only are characterized by internal secretory elements; thus *Altingia* and *Liquidambar* have resin-canals, at the periphery of the pith of the branch, which can be traced into the finest veins of the leaf, and are also met with in the root, where they apparently occur in the phloem. Lastly, mention may be made of special anatomical characters belonging to certain genera or species, viz.: hypoderm in the leaf (*Altingia*), gelatinization of the epidermis of the leaf (*Rhodoleia*), and spicular cells of varied nature in the mesophyll (*Distylium, Sycopsis, Dicoryphe, Hamamelis, Loropetalum, Eustigma, Rhodoleia, Disanthus, Bucklandia*).

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[1] The above-mentioned groups (the Hamamelidoideae, &c.) refer to the classification of the Hamamelideae by Niedenzu in the Natürliche Pflanzenfam.; Bentham and Hooker do not divide the Order into tribes. The Bucklandioideae include the Bucklandieae with *Disanthus, Bucklandia* and *Rhodoleia*, and the Altingieae with *Liquidambar* and *Altingia*; the whole of the remaining genera form the group, Hamamelidoideae. It may also be mentioned here that the anomalous genera, *Ostrearia* and *Myrothamnus* are discussed separately in an appendix to the Order.

[2] See previous note.

2. Structure of the Leaf. The following account is based on the work of Reinsch [1] and Thouvenin, and on my own observations.

The **epidermis** of the leaf usually consists of one layer. **Hypoderm** occurs only in *Altingia excelsa*, Nor. and *A. chinensis*, Oliv., below the epidermis on the upper side of the leaf. Mucilaginous epidermal cells have been observed in *Rhodoleia Championi*, Hook. and *R. Teysmanni*, Miq., cork-warts on both surfaces of the leaf in *Altingia excelsa*. As regards other features, the various species and genera differ in the height and breadth of the epidermal cells in transverse section, in the lateral margins of these cells as seen in surface-view, in the thickening of the walls of the epidermal cells, and in the differentiation of the cuticle. Fairly high epidermal cells occur only in *Bucklandia populnea*, R. Br. The lateral margins of the epidermal cells are straight in *Rhodoleia* and *Bucklandia*; elsewhere they are usually undulated. The outer walls of the lower epidermal cells are produced as papillae in *Rhodoleia Championi*. Finally, the cuticle is very strongly developed in *Corylopsis*, *Dicoryphe*, *Trichocladus*, *Rhodoleia* and *Bucklandia*; it is mostly finely granulated; striation of the cuticle has not been observed.

The **stomata** are found exclusively on the lower side of the leaf. They lie in the plane of the surface of the leaf; each stoma is accompanied on both sides by one or two subsidiary cells, which are parallel to the pore.

The **mesophyll** is always bifacial in structure. The palisade-tissue consists of one layer (species of *Parrotia*, *Fothergilla*, *Corylopsis*, *Hamamelis*, *Disanthus*), or of two layers (species of *Distylium*, *Sycopsis*, *Trichocladus*, *Loropetalum*, *Eustigma*, *Bucklandia*, *Altingia*, *Liquidambar*), or of several layers (*Rhodoleia*). The spongy tissue usually possesses large lacunae. The occurrence of spicular cells in the mesophyll is very common. They appear under different forms. Branched spicular cells of short gnarled shape, lying in the middle of the mesophyll, are characteristic of the very closely related genera *Bucklandia* and *Rhodoleia*. A second form of spicular cells is represented by columnar cells with thick walls, and occasionally branched, and mostly elongated in the same direction as the palisade-tissue, one end being applied to the epidermis in the form of a foot (*Hamamelis virginica*, L. and *Eustigma oblongifolia*, Gardn. et Champ.); a third form consists of sclerenchyma-fibres, which run irregularly in the mesophyll, and either have very thick walls and narrow lumina (*Dicoryphe stipulacea*, St. Hil.) or relatively wide lumina (*Distylium indicum*, Benth., *D. racemosum*, Sieb. et Zucc., *Loropetalum* and *Sycopsis*). According to Niedenzu, spicular cells also occur sparingly in the leaf of *Disanthus*.

In the majority of the genera (*Parrotia*, *Fothergilla*, *Distylium*, *Sycopsis*, *Corylopsis*, *Dicoryphe*, *Hamamelis*, *Trichocladus*, *Loropetalum* and *Eustigma*) the vascular bundles of the **veins** are accompanied by strongly developed hard bast, which either encloses the vascular bundle-system as an annular zone (*Hamamelis*), or is applied to the phloem in the form of an arc. In *Rhodoleia*, *Bucklandia*, *Altingia* and *Liquidambar* the hard bast is only slightly developed, or (*Bucklandia*) is absent. In the larger leaf-veins of *Altingia* and *Liquidambar* (but not in *Hamamelis* [2]) the fibro-vascular system is differentiated as a ring of wood and bast, while in the remaining genera it only forms an arc. Rings of wood and bast (to the number of five, arranged in the form of a horse-shoe), according to Petit, also occur in the uppermost portion of the

[1] Reinsch's investigations extend to the genera: *Parrotia*, *Fothergilla*, *Sycopsis*, *Corylopsis*, *Dicoryphe*, *Hamamelis*, *Trichocladus*, *Loropetalum*, *Eustigma*, *Rhodoleia*, *Bucklandia*, *Altingia* and *Liquidambar*.

[2] According to my own investigation of *H. japonica*, Sieb. et Zucc., and contrary to Reinsch's statement. Reinsch incorrectly describes the rings of wood and bast, which enclose a pith, as concentric bundles.

petiole of *Liquidambar orientale*, while a transverse section of the petiole near its base exhibits only one ring of wood and bast, and at the base itself three vascular bundles.

Oxalate of lime is excreted in the form of ordinary solitary or clustered crystals. The result of Reinsch's investigations are very noteworthy in their systematic bearing, since they established the fact that only clustered crystals occur in the mesophyll of those Hamamelideae with two or more ovules in each loculus of the ovary, i.e. in *Rhodoleia, Bucklandia, Altingia* and *Liquidambar*, while exclusively solitary crystals are found in this tissue in the genera with only one ovule in each loculus (the remaining genera, see p. 329, note 1). In the veins a form of crystal occasionally appears, differing from that found in the ground-tissue of the leaf; thus in *Altingia* and *Liquidambar* small crystals occur along the vascular bundles, whilst in *Hamamelis* and *Corylopsis* there are a few clustered crystals side by side with numerous solitary crystals in this region. The clustered crystals of the mesophyll are mostly large; in *Rhodoleia* and *Bucklandia* they are not numerous. The solitary crystals of the mesophyll vary in size. The large solitary crystals, which together with others of small size occupy correspondingly large cells of the palisade-tissue, give rise to numerous distinct transparent dots in the leaf in species of *Parrotia, Fothergilla, Corylopsis, Trichocladus* and *Loropetalum*.

The **hairy covering** is composed solely of clothing hairs. The latter are for the most part tufted or stellate hairs; e.g. on the leaf of *Parrotia, Fothergilla, Trichocladus* and *Loropetalum*, according to Reinsch, on the leaf of *Eustigma oblongifolium*, Gardn. et Champ., and on other organs in *Sycopsis Griffithiana*, Oliv. and *Distylium racemosum*, Sieb. et Zucc., according to my own observations, and lastly, in *Maingaya*, according to Oliver. The tufted or stellate hairs consist of a variable number of ray-cells, which mostly have thick walls and narrow lumina, and more rarely (*Parrotia*) show less thickened walls; they are either sunk in groups in the epidermis, or occasionally are inserted on a stalk. The ray-cells are either free nearly to the base, or are fused with one another basally for some distance, the latter in *Trichocladus ellipticus*, Eckl. et Zeyh. and *Fothergilla*. According to Thouvenin, simple unicellular trichomes of some length, and with pointed ends, occur on the branch of *Liquidambar styraciflua*. Uniseriate trichomes and glandular hairs, on the other hand, have not been observed in any member of the Order. The glandular leaf-teeth of *Liquidambar styraciflua* contain the termination of a vascular bundle, as well as numerous cells filled with tanniniferous mucilage, and bear stomata on their upper surface (Reinke).

3. STRUCTURE OF THE AXIS[1]. In most members of the Order the formation of **cork** takes place early; in *Bucklandia* and *Rhodoleia* alone the cork does not arise until a late stage. In the cases investigated by Reinsch (species of *Hamamelis, Trichocladus* and *Liquidambar*) and by me (species of *Distylium, Disanthus* and *Liquidambar*) the cork develops from the subepidermal cell-layer. The cork-cells have thin walls throughout. In the transverse section of the branch, Reinsch distinguishes high, quadrangular cork-cells, which form the spongy cork of the genera *Parrotia, Distylium* and *Sycopsis*, and tabular cork-cells, which are low in the radial direction, and are distinctive of the cork in the remainder of the genera investigated by him. It must, however, be borne in mind in this connexion that the cork-cells in the thicker branches occasionally (species of *Hamamelis, Trichocladus* and *Liquidambar*) show different dimensions in the same transverse section, those formed in the spring having wide lumina, whilst those arising later in the

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[1] **Most important literature: Reinsch and Solereder, ll. cc.**

season become gradually flatter. Phelloderm-formation occurs (*Corylopsis, Dicoryphe, Trichocladus, Liquidambar*).

The primary **cortex**, especially its middle portion, is differentiated as collenchyma in many cases. It sometimes (species of *Distylium, Sycopsis, Dicoryphe, Bucklandia, Altingia, Liquidambar*) includes sclerotic cells.

In all the genera investigated by Reinsch, and to these I can add *Disanthus*, the pericycle is formed by a composite sclerenchymatous ring, which is continuous in most of the genera, being interrupted in *Altingia* and *Liquidambar* only. Secondary hard bast is rare (occurring in *Fothergilla, Distylium* and *Sycopsis*, according to my own observation; in *Liquidambar*, according to Möller; 'sclerenchyma in the leptom,' in *Dicoryphe* and *Sycopsis*, according to Reinsch). The medullary rays of the bast, like those of the wood, are narrow.

The structure of the **wood**[1] is very uniform and characteristic. In a transverse section one observes narrow, uni- or bi-seriate medullary rays, scattered vessels never with wide lumina, which are four- or more-sided, more rarely (*Trichocladus*) round, and wood-prosenchyma, which as a rule has thick walls and narrow lumina, and forms the groundwork of the wood. The vessels are characterized by strongly inclined division-walls, having scalariform perforations, with many bars; the number of bars, for example, amounts to 8–14 in *Parrotia persica*, C. A. Mey., to as many as 13 in *Hamamelis virginica*, L., as many as 22 in *Liquidambar styraciflua*, L., 30–40 in *Bucklandia populnea*, R. Br., sometimes more than 40 in *Corylopsis pauciflora*, Sieb. et Zucc. The walls of the vessels where they are in contact with medullary rays are provided with simple pits, side by side with which transitions to bordered pits occur. Spiral thickening has only been observed on the ends of the vessels of *Corylopsis himalayana*, Griff., *C. pauciflora*, Sieb. et Zucc., *C. spicata*, Sieb. et Zucc. and *Rhodoleia Championi*. The wood-prosenchyma bears bordered pits; in *Corylopsis* the borders of these pits attain a diameter of ·0045 mm., in *Hamamelis* and *Sycopsis* a diameter of ·007 mm., that is to say, they are of large size. In *Hamamelis chinensis*, R. Br., the walls of the prosenchyma are strengthened by means of a spiral band. With regard to the medullary rays, it remains to be mentioned that their cells are elongated either in the radial or in the vertical direction; in the second case they are of considerable height.

Reinsch makes a number of statements regarding the structure of the **pith**. According to him, the pith is homogeneous in most cases (including *Liquidambar formosana*). A heterogeneous pith has been demonstrated only in *Liquidambar styraciflua* and *L. orientale*. Reinsch moreover points out that in some members of the Order, e. g. in *Liquidambar* and *Altingia*, or in *Hamamelis* and *Corylopsis*, the cells of the pith are transversely elongated in longitudinal section (i. e. elongated transversely to the vertical direction), whilst in other cases, e. g. in *Bucklandia* and *Rhodoleia*, they are longitudinally elongated.

The crystalline cell-contents in the axis are the same as in the leaf. The sharp systematic distinction which exists in the occurrence of solitary or clustered crystals in the ground-tissue of the leaf, does not hold good in the same manner for the axis.

Special internal **secretory organs** occur in the form of resin-canals, only in the two very closely allied genera *Altingia* and *Liquidambar*. There are 7–8 of these resin-canals situated at the margin of the pith, and they lie so near to the protoxylem of the vascular bundles that they might be, and actually have been, interpreted as an integral part of the latter. They are surrounded

[1] The structure of the wood has been investigated by me in the genera *Parrotia, Fothergilla, Distylium, Sycopsis, Corylopsis, Hamamelis, Trichocladus, Disanthus, Rhodoleia, Bucklandia, Liquidambar* and *Altingia* (see 'Holzstruktur,' l. c.), and recently also in *Dicoryphe stipulacea*, St. Hil. and *Eustigma oblongifolium*, Gardn. et Champ.

by several layers of small-celled epithelium, and are of schizolysigenous origin, according to Sieck. The balsam-canals of the axis can be traced from the branches into the leaves, where they likewise stand in relation to the vascular bundles, being situated on the upper side of the xylem; they can be traced into the finest branches of the veins. In tissues other than the margin of the pith, the resin-canals do not occur [1], but, according to Planchon and Van Tieghem, cells filled with resin, but not differentiated as idioblasts, occur in the secondary cortex of the branch. The resin-canals are present in the root. In the young root they lie on the inner side of the groups of primary bast of the bundle-system, whilst in the older root they come to be situated between the primary and secondary bast, owing to the fact that the cambium-ring extends on the inner side of them; in consequence of this they appear to belong to the bast, and subsequently, when the primary bast is compressed after the manner of horn-bast, they seem to lie in the pericycle. In addition to the resin-canals, the same type of secretory cells is found in the bast of the root as in the branch [2].

APPENDIX: ON THE GENERA *Ostrearia* AND *Myrothamnus*.

Of the two genera, which belong to the doubtful Hamamelideae, I was able to investigate an original specimen of *Ostrearia* in the Kew Herbarium (*O. australiana*, Baill., Rockingham Bay, misit F. v. Müll.) anatomically. The anatomical investigation proved that this genus, which even in the structure of its fruit agrees quite well with *Parrotia*, *Hamamelis*, &c., belongs without doubt to the Hamamelideae. The xylem is quite similarly constituted to that of the Order in question. The medullary rays are uniseriate, the wood-prosenchyma has thick walls and narrow lumina, and bears bordered pits, the vessels have relatively small lumina, are quadrangular and scattered in a transverse section, and provided with scalariform perforations having very numerous bars, and have large simple pits in contact with the parenchyma of the medullary rays. As in the Hamamelideae, the pericycle contains a composite and continuous ring of sclerenchyma. As regards the structure of the leaf the following features favour the inclusion of *Ostrearia* amongst the Hamamelideae: the absence of external glands, the bifacial leaf-structure, the stomata, which only occur on the lower side of the leaf and are accompanied by subsidiary cells placed parallel to the pore, and also the occurrence of sclerenchyma-fibres in the mesophyll, traversing the leaf-tissue in a perpendicular direction and branching below the epidermis on both sides. Trichomes have not been observed in *Ostrearia*. Oxalate of lime is found accompanying the sclerenchymatous sheath of the vascular bundles in the form of ordinary solitary crystals; in the mesophyll it occurs in the form of clustered crystals.

The second genus *Myrothamnus*, both species of which, viz. *M. flabellifolia*, Welw. and *M. moschata*, Baill., I was able to examine at Kew, must certainly be excluded from the Hamamelideae, in accordance with the anatomical structure, as well as the exomorphic features. Provisionally, until a definite relation to some other Order has been established, it may be best to regard the genus *Myrothamnus* as forming a separate independent Order, as has been done in the Natürliche Pflanzenfamilien. Anatomically, *Myrothamnus* is essentially distinguished from the rest of the Hamamelideae by the possession of spherical resin-cells, which occur in the epidermis on both sides of the leaf, and penetrate somewhat into the mesophyll; further, by the stomata, which are surrounded in an irregular manner by several ordinary epidermal cells, by the bordered pitting of the vessel-wall in con-

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[1] Tschirch's statement to the contrary (Angew. Pflanzenanat., Bd. i, 1889, pp. 501, 502), according to which the Liquidambareae possess schizogenous secretory receptacles in the primary cortex, is incorrect.

[2] The officinal 'Styrax liquidus,' which, as is well known, is obtained by boiling the bark of *Liquidambar orientalis*, Mill. in water, and likewise the 'sweet gum' of *L. styraciflua*, L. are, according to J. Möller and Planchon (Zeitschr. österr. Apothek.-Ver., Bd. l, 1896, Heft 1, 2), not the product of the above-mentioned resin-canals, but are of pathological origin, similarly to the resin of *Styrax Benzoin*. In consequence of injuries and other mechanical influences, schizogenous balsam-cavities arise in the wood, their further development being lysigenous; the balsam from these cavities only secondarily permeates the cortex.

tact with the parenchyma of the medullary rays, and also by the compound pollen-grains [1], which consist of four cells arranged tetrahedrally.

The following points regarding the structure of the leaf and of the wood may be added to complete the anatomical diagnosis of *Myrothamnus*. The leaf-structure is centric. The vascular bundles of the veins are embedded and only accompanied by a little sclerenchyma. Trichomes are wanting. Oxalate of lime occurs in the leaf in the form of clustered crystals. A transverse section of the wood, like that of the Hamamelideae, shows vessels with very small quadrangular lumina, uniseriate medullary rays, and wood-prosenchyma having thick walls and fairly narrow lumina and bearing bordered pits. The bordered pits of the vessels are exceptionally small in *Myrothamnus*. The perforations of the vessels are in part scalariform with many bars, as in the Hamamelideae. Besides these, what are called pit-perforations occur; in this case the cross-wall bears innumerable small elliptical perforations of the same size as the border of the pits on the vessels; these perforations are arranged parallel to the transverse axis of the division-wall, and hence are also placed in parallel rows with regard to one another. The thickening ridges between the small pit-like perforations of the same row are frequently so delicate that, on superficial observation, the perforation appears to be scalariform.

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BRUNIACEAE.

1. Review of the Anatomical Features. This Order is characterized by a series of anatomical features in the structure of the leaf and axis. The stomata are surrounded by several epidermal cells undifferentiated in shape. The vascular bundles of the leaves are embedded. The wood is characterized by narrow medullary rays, by vessels having relatively small lumina, scalariform perforations in their end-walls, and bordered pits on the walls in contact with the parenchyma of the medullary rays, by scanty development of wood-parenchyma, and by the distinct bordered pitting of the wood-prosenchyma. The formation of cork is superficial. The pericycle contains primary bundles of hard bast, which are sometimes more or less united by means of groups of stone-cells. The hairy covering consists of simple, unicellular hairs of varied length. Glandular hairs are absent; internal glands likewise. Oxalate of lime occurs in the form of solitary and clustered crystals.

2. Structure of the Leaf. The structure of the leaves has been described by Thouvenin [2] and Niedenzu [3]; the leaves usually resemble those of *Erica* or *Cassiope*, more rarely those of *Thymus* or *Myrtus*, and are frequently adpressed to the stem and xerophilous. They are traversed by three longitudinal veins—a median vein and two small lateral strands.

The **epidermis** on both sides of the leaf is composed of large cells above and below the median vein; from this region the size of the epidermal cells

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[1] Pollen-grains of this kind do not occur in any genus of the Hamamelideae.

[2] Ann. sc. nat., sér. 7, t. xii, 1890, pp. 148–52 and pl. 22. Thouvenin's investigations extend to species of *Audouinia*, *Berardia*, *Brunia*, *Linconia*, *Staavia* and *Tittmannia*.

[3] In Natürl. Pflanzenfam., iii. Teil, Abt. 2, 1891, pp. 132, 133.

diminishes towards the margin of the leaf. The epidermal cells are more or less arched outwards, sometimes as papillae (Niedenzu), and have a polygonal or slightly undulated outline in surface-view. The cuticle is usually very thick, being occasionally smooth, but it may also be longitudinally striate, e.g. in *Brunia lanuginosa*, *B. arachnoidea*, or *Berardia paleacea*. Niedenzu also mentions silicification of the epidermis.

As a rule the **stomata** occur on both surfaces of the leaf, in *Linconia cuspidata* on the lower side only. They occupy the space between the median vein and the leaf-margin, either forming a single fairly regular longitudinal row, e.g. in *Brunia lanuginosa*, or two such rows (*Brunia arachnoidea*, *Tittmannia lateriflora*, *Audouinia capitata*), or 4–5 (*Linconia cuspidata*, *Berardia paleacea*, *Staavia radiata*). The long axis of the stomata, which coincides with the pore, lies in the direction of the median vein in nearly all the genera; an exception to this is afforded by *Staavia radiata* alone, in which the long axis of the stomata is placed at right angles to the median vein. The guard-cells are surrounded by 4–7 cells, which are somewhat smaller than the remaining epidermal cells; the arrangement of these subsidiary cells, as in *Heuchera*, appears to be spiral in accordance with their development.

The **assimilatory tissue** is mostly centric in structure, the central part of the cross-section of the leaf being occupied by the vascular bundle and the spongy parenchyma surrounding it. Between the spongy parenchyma and the epidermis a row of parenchymatous palisade-cells is found on all sides of the transverse section. Occasionally, however, according to Niedenzu, true palisade-tissue is situated on the lower side of the leaf only.

Libriform is wanting in the xylem of the vascular bundles of the **veins**. Hard bast accompanying the vascular bundles is either not developed or is produced in varying abundance.

Thouvenin observed solitary crystals of **oxalate of lime**, accompanying the vascular bundles in *Brunia*, *Berardia*, *Audouinia* and *Tittmannia*. Niedenzu states that clustered crystals occur much more frequently than solitary crystals in this Order.

The occurrence of branched fibrous sclerenchyma-cells in the mesophyll of *Linconia cuspidata* is worthy of note (Thouvenin).

The **hairy covering**, which frequently occurs on the leaves and in the floral region, is constituted by very long, slender, unicellular hairs, with a thick, smooth wall, and a narrow lumen. Side by side with these, short unicellular, thick-walled hairs sometimes (*Audouinia capitata*) also occur.

3. STRUCTURE OF THE AXIS[1]. In the anatomical structure of the **wood**, genetic relations to the Cornaceae and Hamamelideae can be very clearly recognized. Thus the wood, as in these Orders, is characterized by scalariform perforations in the vessels, with many or even very abundant bars, and by wood-prosenchyma with typically bordered pits (the latter feature is described by Thouvenin also for *Berardia paleacea* and *Staavia radiata*). The medullary rays of the wood are as much as 3 cells in breadth; the vessels do not have large lumina (diameter reaching ·045 mm.), and are mostly isolated. The wall of the vessels, even where bounded by ray-parenchyma, bears bordered pits, which sometimes have the form of scalariform bordered pits. The wood-parenchyma is restricted to the neighbourhood of the vessels, or occurs only to a subordinate extent among the prosenchyma.

Thouvenin makes the following statements regarding the **cortex**. The epidermis consists of cells which are arched outwards convexly, and bears the simple hairs already described. The thin-walled cork arises immediately

[1] Solereder, Holzstruktur, 1885, pp. 118, 119; species of *Raspalia*, *Berzelia*, *Brunia* and *Audouinia* were investigated. See also Thouvenin, loc. cit.

below the epidermis. The primary cortex is formed by only a few rows of cells, and in the species of *Brunia*, *Berardia*, *Staavia* and *Tittmannia*, already named, contains sclerosed cells. In *Audouinia capitata* isolated bundles of primary bast-fibres occupy the boundary between bast and primary cortex; in the remaining genera investigated by Thouvenin, there is an interrupted sclerenchymatous ring, consisting of groups of bast-fibres and of stone-cells. The bundles of soft bast are narrowed outwards in the transverse section in such a manner that the medullary rays between them broaden out externally in the form of wedges.

HALORAGEAE.

The Halorageae, which are placed near the Onagrarieae by most systematists, are distinguished from that Order by the lack of intraxylary phloem [1]. They are further characterized by the absence of a special type of stoma, and by the simple perforations of the vessels. Oxalate of lime is excreted in the form of clustered crystals. Internal secretory organs are absent. The hairy covering is formed by simple, unicellular or uniseriate trichomes, peltate hairs, glandular shaggy hairs, and other external glands of complicated structure. Some of the Halorageae are water-plants, and in these an elaborated intercellular system as well as reduction of the fibro-vascular system is found. Of the terrestrial members, the species of *Gunnera* have an anomalous structure, in so far as steles occur in place of the vascular bundles; these steles anastomose to form a network in the more strongly developed stems of certain species.

The **mesophyll** may be differentiated into palisade and spongy tissue, being bifacial or subcentric in structure, or may consist of uniform parenchymatous tissue. The **stomata**, as already stated, lack characteristic subsidiary cells. The cells adjacent to the stomata, however, occasionally differ in size and shape from the rest of the epidermal cells. The development of the stomata takes place according to the Cruciferous or Ranunculaceous type (Parmentier). As regards the occurrence of stomata, the amphibious species behave like the water-plants belonging to other Orders. Numerous stomata occur when air is the surrounding medium; they are absent or diminish in number on the corresponding surface when the leaf is developed under water.

Thus, according to Hegelmaier, in the land-forms of the *Eucallitriches* the stem and both leaf-surfaces are rich in stomata; in the submerged forms stomata are absent on the stem and only occur sporadically on the leaves; in the floating leaves they are numerous on the upper side (see also H. Schenck). According to Goebel, a deep-water form of *Hippuris vulgaris* bore two large stomata only at the incurved tip of the leaf; the land-form of the same species has numerous stomata. Finally, in those species of *Myriophyllum* which have been carefully examined, the water-form has no stomata, while the land-form has numerous stomata on both sides of the leaf [2].

Ephemeral stomata have been observed by Borodin in *Callitriche*. The submerged *Callitriche autumnalis* possesses a group of 3–8 stomata rather towards the lower side of the tip of the young leaf, where the median vein dies out; these stomata subsequently become resorbed, and in their place an opening in the epidermis appears. In like manner the tip of the leaf of *C. verna* bears one very large stoma, which likewise subsequently disappears.

[1] Parmentier's statement as to the occurrence of intraxylary soft bast in *Haloragis* and *Loudonia* pro parte is doubtless incorrect.

[2] Parmentier's observations, according to which stomata occur on both sides of the leaf of *Myriophyllum mexicana*, on the upper side only in *M. elatinoides* etc., and so on, require further examination with reference to the habitat of the plant.

The original function of these ephemeral stomata has still to be investigated, and is possibly similar to that of the stomata on the lobes of the leaf in *Gunnera scabra*, *G. macrophylla*, and probably also *G. manicata*, which have been described by Reinke, Merker, and Berckholtz. These are 'water-pores' or 'mucilage-pores'. Numerous stomata occur on the upper side of the laciniae in the above-named species of *Gunnera*, but only a few on the lower side. Below the former, small-celled parenchyma is found, and beneath that the vascular strands. The small-celled parenchyma is filled with mucilage, which, as Merker has demonstrated in *Gunnera scabra*, makes its way into the intercellular spaces, and is excreted externally through the stomata. As soon as the leaf has unfolded, the formation of mucilage ceases, and the laciniae wither.

Oxalate of lime is differentiated in the form of clustered crystals, as has already been stated above. A very peculiar feature is the occurrence of spiny clustered crystals, which lie in small thin-walled cells, completely adapted to the shape of the clusters; these cells border and project into the intercellular spaces in *Myriophyllum* (Vöchting and others) and *Serpicula repens*, L. (Fig. 72, *A*). Nuclear crystalloids have been met with in the epidermis of the leaf and stem of *Hippuris vulgaris* by Zimmermann.

Among the **trichomes**, the simple hairs may be referred to first. They are unicellular (*Gunnera*, *Haloragis alata*, Jacq.) or uniseriate and few-celled (*Serpicula*). The unicellular hairs of *Gunnera manicata* (according to Berckholtz) and *Haloragis* are short, and possess subsidiary cells, which, like the body of the hair, are silicified. Peltate hairs (Fig. 72, *B–D*) are found in *Hippuris* and *Callitriche* (Hegelmaier, Rauter and O. Bachmann); functionally, at least in some cases (in *Callitriche*, according to Schilling) they are mucilage-glands. The shield is small, and has thin walls, more or less numerous rays, and an entire, or a crenate margin, owing to the projection of the rays. The shield is borne by one or several stalk-cells.

The principal rays of the shield vary in character, occasionally even in the same species. In some cases they consist of simple ray-cells (*Hippuris maritima*, Hellen.). In other cases they are divided by secondary radial walls (*Hippuris vulgaris*, L., *Callitriche obtusangula*, Le Gall., *C. platycarpa*, Kütz., *C. stagnalis*, Scop., *C. terrestris*, Rafin., *C. verna*, L., *C. Wightiana*, Wall.). In a third series of species (*C. autumnalis*, L., *C. truncata*, Guss., *C. verna*, L.) they are divided by secondary tangential walls, and in *Hippuris vulgaris* by secondary radial and tangential walls; in these cases the tangential walls correspond with one another in such a way that the shield appears to be composed of concentrically arranged zones of cells.

A modification of the peltate hairs is found in the fan-shaped trichomes (Fig. 72, *D*) occurring in the axils of the leaves of *Hippuris vulgaris*, according to Rauter; a stalk-cell bears a vertically placed fan, which consists of a layer of cells radiating from the stalk-cell.

The glandular shaggy hairs of *Myriophyllum* and *Gunnera* may be classed next to the peltate hairs. In *Myriophyllum*, where Borodin first observed them, they are found on the terminal portions of the leaves and leaf-segments (Fig. 72, *E*), at the points of insertion of the pinnules, and on the stem between the bases of the leaves. They are flask-shaped, and consist of a large number of polygonal cells, containing strongly refractive bodies of oily appearance, and of a glucoside-like nature (according to Raciborski). These shaggy hairs are evident only on the young shoots; they subsequently wither. Within the genus *Gunnera* glandular shaggy hairs of similar structure are described by Merker in *G. scabra*, where they excrete mucilage, are derived from a single epidermal cell, and likewise shrivel up after a time, and by Berckholtz in *G. manicata*. Other forms of external glands are the structures which are described as colleters by Merker, and have been observed on the

leaves of *Gunnera scabra*, *G. macrophylla* (Fig. 72, *F*) and *G. manicata*. They are more or less distinctly hemispherical warts, which consist of a considerable number of epidermal cells, arranged in longitudinal section, in the form of a fan, and adjoined internally by a few isodiametric parenchymatous cells. The rather strongly swollen outer wall of the secretory epidermal cells is covered by the cuticle, which becomes raised up, and is finally burst by the excreted tanniniferous mucilage. According to Merker, the colleters occurring on the ribs of the leaves of *G. scabra* are specially large; they are further distinguished by the papillose differentiation of their secretory epidermis. According to Berckholtz, similar trichomes, i.e. hemispherical structures with palisade-like, papillose epidermis, occur on the leaf-surface of *Gunnera manicata*, side by side with those of a secretory nature; these structures are, however, without secretion, and may therefore be simply described as warts;

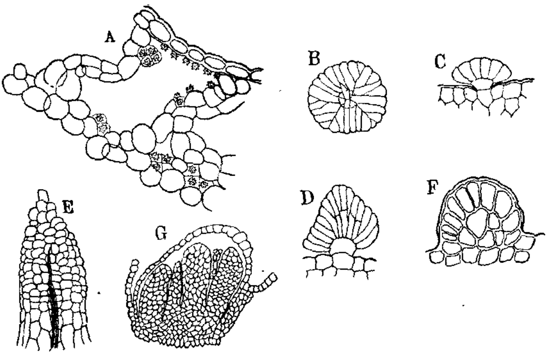

FIG. 72. A, Transverse section through a piece of the cortex of *Serpicula repens*, L. B–D, Peltate hairs of *Hippuris vulgaris*, L.; B in surface-view, C in section; D, fan-shaped peltate hair. E, Tip of a segment of the leaf of *Myriophyllum verticillatum*, L. F, Colleter from the leaf of *Gunnera macrophylla*, Bl. G, Longitudinal section through a stem-gland of *Gunnera macrophylla*.—A and B Original, B–D after Rauter, F and G after Merker.

their cell-walls are silicified. We may now discuss the stem-glands (Fig. 72, *G*) occurring between the leaf-bases in *Gunnera macrophylla* and *G. scabra*. These glands are composed of several structures, resembling shaggy hairs (glandular laciniae), leaving only narrow canals between them, and clothed by a common cap-shaped layer of epidermal cells. The glandular laciniae are composed of numerous polygonal cells. When the gland begins to be active, the outermost cells of the glandular laciniae swell up and become mucilaginous. Owing to the pressure of the masses of mucilage, which accumulate in this manner, and likewise contain tannin, the epidermal cap finally bursts. As is well known, these stem-glands are connected with the intrusion of colonies of *Nostoc*, which are found enclosed in the superficial part of the stem in species of *Gunnera*; the species of *Nostoc* concerned, originally named *N. Gunnerae* by Reinke, is, according to Bengt Jönsson, identical with *N. punctiforme*, (Kütz.) P. Hariot. In connexion with the external

glands, it may be remarked that the spines on the stalks and ribs of the leaves (*G. manicata* and *G. scabra*) are emergences.

The **axis** shows varied structure, apart from the general features, which have already been referred to above. A slender central cylinder, surrounded by a thick lacunar cortex, is characteristic of the aquatic species. *Hippuris* and *Myriophyllum* have the simplest and most reduced structure; in these plants the centre of the stem is occupied by an axile fibro-vascular mass, and a true pith is wanting here. The pith, exhibited by the older stems in both genera, only arises subsequently by the resorption of the central primary vessels of the fibro-vascular mass—hence it is equivalent to wood-parenchyma. As compared with *Hippuris* and *Myriophyllum*, *Callitriche* represents a less reduced type, inasmuch as true pith is present, although it is restricted to two or three cells. The land-plants, as a rule, exhibit normal stem-structure with a ring of cambium and secondary development of wood (*Haloragis alata*, Jacq., *Loudonia aurea*, Lindl.). The stems of the species of *Gunnera*, on the other hand, have anomalous structure; they have been investigated by Reinke,

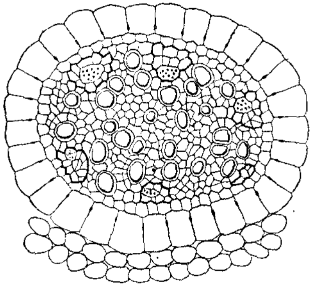

FIG. 73. Transverse section through one of the inner steles of the stem of *Gunnera chilensis*.—After Van Tieghem and Douliot.

Merker, and especially by Van Tieghem and Douliot. The stem of *Gunnera* is polystelic in structure, as Van Tieghem expresses it. A transverse section of the stem through the higher internodes shows a larger or smaller number of variously orientated steles, i.e. rings of vascular bundles, with or more frequently without pith.

The hypocotyledonary portion possesses only a single stele without pith. In like manner in the species with weakly developed stems (*G. cordifolia*, *G. monoica*, *G. prorepens*), only one stele is present even in the higher internodes. In other species (*G. integrifolia*, *G. lobata*, *G. magellanica*), the single stele divides in the higher internodes into 3 or 4, which are arranged in the form of a ring in transverse section, and have a circular or band-shaped cross-section. In other species having still thicker stems (*G. macrophylla*, *G. perpensa*), a larger number of steles is met with in transverse section; together, however, they form a circle. Finally, the steles in *G. bracteata*, *G. chilensis*, *G. commutata*, *G. insignis*, *G. manicata* and *G. petaloidea* are still more numerous and are scattered quite irregularly over the cross-section of the stem. When several steles occur, they invariably form a network. Further, the steles, whatever their number and arrangement may be, always possess the same structure (Fig. 73). They are enclosed by an endodermis, characterized by the presence of Caspary's dots on the radial walls; below the endo-

dermis they have a pericycle one or two cells broad; then follows a ring of from two to six isolated groups of soft bast, and still further inwards are the vessels, which are usually embedded in thin-walled parenchyma, while pith is usually absent. Lastly, it may be mentioned that the fibro-vascular system passes out of the axis into the leaf in the form of steles.

With regard to the primary **cortex** it has already been stated that it contains numerous air-cavities in the aquatic species. In *Hippuris* these cavities are numerous, isodiametric in transverse section and separated by one-layered plates of cells; in *Myriophyllum* and *Serpicula* they are arranged in a ring in transverse section, and are radially elongated. The cortex of *Loudonia aurea* contains subepidermal groups of cells resembling bast-fibres, and palisade-tissue; in *Haloragis* the epidermis and the outermost cell-layer of the cortex consist of sclerosed cells. The pericycle in the water-plants is surrounded by a more or less distinct endodermis; in *Haloragis alata* and *Loudonia aurea*, and likewise in *Proserpinaca* according to Parmentier, the pericycle is formed by isolated groups of sclerenchymatous cells; the latter are of the nature of rod-cells in *Haloragis*. As regards the structure of the wood of *Haloragis alata*, the medullary rays are narrow, the vessels have narrow lumina (diameter = ·028 mm.) and simple perforations, the wall of the vessels has bordered pitting where it is in contact with the parenchyma of the medullary rays, and the wood-prosenchyma has fairly thick walls, narrow lumina, and simple pits. The medullary tissue is either lacunar or the central portion disappears.

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RHIZOPHORACEAE.

1. Review of the Anatomical Features. The Rhizophoraceae are characterized anatomically by stomata surrounded by several epidermal cells, by the lack of glandular hairs on the foliage-leaves, and by the tendency to the formation of scalariform perforations in the vessels. In the genera of the tribe Rhizophoreae the perforations of the vessels are, so far as is known, exclusively scalariform, in the genera of the Legnotideae they are simple and scalariform. The wood-prosenchyma bears simple pits in the Rhizophoreae, bordered-pits in the Legnotideae. It still remains to be determined how widely the superficial formation of cork and the composite and

continuous sclerenchymatous ring in the pericycle are distributed in the Order. Oxalate of lime is excreted in the form of clustered and ordinary solitary crystals. Of internal secretory organs one only finds cells with mucilaginous walls, occurring in the epidermal and internal tissue of the leaf. A hairy covering is rare, and consists of simple unicellular trichomes, which are occasionally (*Macarisia*) grouped to form tufts; glandular shaggy hairs have only been observed on the stipules. Special anatomical features occurring in the Order are the following: idioblasts containing clustered (*Carallia*) or solitary crystals (*Cassipourea, Macarisia, Weihea*) in the integumental tissue of the leaf; development of hypoderm on the upper side of the leaf, especially in the plants of the mangrove formation; H-shaped spicular cells in the ground-tissue of the leaf, axis and root of *Rhizophora*; cork-warts on the leaves (*Carallia, Rhizophora, Weihea*).

2. STRUCTURE OF THE LEAF[1]. The **leaf-structure** is bifacial in most

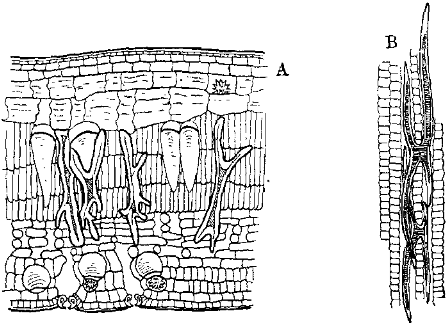

FIG 74. A, Transverse section of the leaf of *Rhizophora conjugata*, L. B, H-shaped spicular cells from the cortex of the branch of *Rhizophora Mangle*, L.—A, Original, B, after Warming.

members of the Order. Species of *Anisophyllea* and *Ceriops*, according to Schimper, as well as *Kandelia Rheedii*, W. et A., show a tendency to centric structure. The palisade-tissue frequently consists of several layers of short cells (*Ceriops Roxburghiana*, Arn.). The spongy tissue mostly possesses large intercellular spaces. In *Weihea zeylanica*, Baill., it is very dense, in *Bruguiera gymnorrhiza*, Lam., collenchymatous. The mesophyll of *Rhizophora* contains spicular cells of two shapes, differentiated as internal hairs. The spicular cells in the palisade-tissue are more or less distinctly H-shaped, while in the spongy tissue they are star-shaped. Both forms occur in *R. conjugata*, L. and *R. mucronata*, Lam., the stellate form in *R. Mangle*, L. alone.

As regards the **integumental tissue**, it may, in the first place, be pointed

[1] According to Schimper, loc. cit., and according to unpublished observations and preparations by Dr. O. Bachmann. The latter extend to the genera *Rhizophora*, *Ceriops*, *Kandelia* and *Bruguiera*, of the Rhizophoreae, and to the genera *Carallia*, *Gynotroches*, *Weihea*, *Macarisia*, *Blepharistemma* and *Cassipourea* of the Legnotideae; the species investigated will be named in the text in connexion with the anatomical features.

out that the epidermis on the upper side of the leaf rarely represents a simple layer; occasionally it is two-layered locally or throughout, and frequently it is supplemented by the formation of hypoderm.

The epidermis on the upper side of the leaf of *Carallia integerrima*, DC., *Weihea zeylanica*, Baill. and *Blepharistemma corymbosum*, Wall. consists of one layer; it is two-layered in places, owing to the appearance of division-walls parallel to the surface of the leaf, in *Cassipourea elliptica*, Poir., *C. guianensis*, Aubl. and *C. Spruceana*, Benth. The following species have a hypoderm of one layer: *Bruguiera eriopetala*, W. et A. and *B. gymnorrhiza*, Lam., as well as *B. caryophyllaeoides* and *B. parviflora*, according to Schimper; further *Gynotroches axillaris*, Bl. and *Macarisia* sp. (Hildebrandt, no. 3228), and, according to Schimper, *Crossostyles multiflora*, A. Br.; there is a hypoderm of two layers in *Ceriops Candolleana*, according to Schimper; a hypoderm of three or more layers in *Rhizophora conjugata*, L., *R. Mangle*, L. and *R. mucronata*, Lam., as well as *Ceriops Roxburghiana*, Arn., *Kandelia Rheedii*, W. et A., and, according to Schimper, *Dactylopetalum Barteri*, Hook. f., have a two-layered epidermis combined with the occurrence of a layer of hypoderm-cells situated below it; even in the mature leaf, the origin of the former from a single layer of cells by the appearance of division-walls parallel to the surface of the leaf is evident. The lumina of the hypodermal cells vary in size, occasionally in the same hypoderm; especially in the inner layers they often attain considerable dimensions.

On the lower side of the leaf a distinct hypoderm is developed in *Bruguiera gymnorrhiza* only. The xerophilous character of the leaf, besides appearing in the formation of a many-layered integumental tissue, finds expression in the often considerable development of the cuticle, and in the occurrence of cells with mucilaginous membranes. The latter have been met with in the upper epidermis of the leaf of *Blepharistemma corymbosa* and *Carallia integerrima*, in the hypoderm on the upper side of the leaf of *Gynotroches axillaris*, and according to Schimper (see Fig. 21, *J*, in the Natürl. Pflanzenfam.) also in *Dactylopetalum Barteri*, Hook. f., in the palisade-tissue of *Rhizophora Mangle* and *R. mucronata*, and in the palisade and spongy tissue of *R. conjugata*.

Stomata are present only on the lower surface of the leaf. They are depressed and are often provided with a front cavity of characteristic shape. In surface-view they are surrounded by several subsidiary cells, which, in the better investigated species of *Ceriops*, *Kandelia*, *Bruguiera* and *Blepharistemma*, are distinguished from the rest of the epidermal cells by their oblong shape, but exhibit no specially characteristic arrangement in the mature leaf. In *Rhizophora Mangle* the walls of the subsidiary cells bounding the respiratory cavities are cuticularized.

The vascular bundles of the smaller **veins** of the leaf are mostly embedded; they are almost transcurrent vertically in *Macarisia* sp. (Hildebrandt, no. 3228), in which their vascular system is enclosed by large, thin-walled parenchymatous cells. Sclerenchyma accompanying the vascular bundles may be either absent (*Rhizophora Mangle*, *Blepharistemma corymbosum*) or present; in the latter case it is usually weakly, and only in rare cases strongly developed in the form of a ring (*Gynotroches axillaris*). Enlarged terminal tracheides have been observed by Schimper in species of *Ceriops*, *Kandelia* and *Bruguiera*.

Oxalate of lime is present in the leaf in the form of clustered crystals or rhombohedra. Clustered crystals are exclusively present or predominate in the genera *Rhizophora*, *Ceriops*, *Kandelia*, *Bruguiera*, *Carallia* and *Gynotroches*; solitary crystals in like manner in *Weihea*, *Macarisia*, *Blepharistemma* and *Cassipourea*. Special emphasis must be laid on the occurrence of oxalate of lime in the epidermis on both sides of the leaf, in *Carallia* in the form of clustered crystals, in *Weihea*, *Macarisia* and *Cassipourea* in the form of solitary crystals. The epidermal cells concerned, like the well-known crystal-cells of

the leaf of *Citrus*, exhibit a considerable thickening of their inner wall, in which the clustered or solitary crystal is embedded.

The **hairy covering** essentially consists only of unicellular, pointed, clothing hairs, with thin or thick walls; they are to be found more frequently on the reproductive than on the vegetative parts. The tufted hairs of *Macarisia* consist of a few such trichomes. Whilst external glands are wanting on the lamina, glandular shaggy hairs occur on the inner side of the stipules in certain species; they excrete a gum-like substance on the leaf-buds. According to Warming, these glandular shaggy hairs consist of a sessile ellipsoid head, composed of a central multiseriate group of cells, sheathed by a secretory epidermis of palisade-like differentiation. The small black spots which are to be met with on the lower side of the leaf of *Rhizophora Mangle*, are not glands, as Warming states, but cork-warts. The latter also occur, for example, in *R. mucronata*, *Carallia integerrima* and *Weihea zeylanica*.

With regard to the structure of the **petiole**, which has been investigated in *Rhizophora Mangle* only, see Warming, loc. cit., Taf. IX–X, Fig. 13.

3. Structure of the Axis. With respect to the structure of the **wood** (which has been investigated amongst the Rhizophoreae in species of the genera *Rhizophora*, *Ceriops*, *Kandelia*, *Bruguiera*, and amongst the Legnotideae in species of the genera *Carallia*, *Gynotroches*, *Macarisia* and *Cassipourea*) the Rhizophoreae, which constitute the species of the mangrove-formation, are essentially distinguished by two features from the Legnotideae, which are the Rhizophoraceae of the dry land. Firstly, the wood-prosenchyma bears simple pits in the Rhizophoreae, bordered pits in the Legnotideae. Secondly, the Rhizophoreae have exclusively scalariform perforations in the vessels, whilst on the other hand, the Legnotideae have simple elliptical (rarely circular) perforations, accompanied by others of the scalariform type, the latter being restricted to the neighbourhood of the primary xylem, or occurring also in the secondary region of the wood. The number of the bars in the scalariform perforations is not very great (not exceeding 12), often less (in *Rhizophora Mangle* not more than 5).

The medullary rays of the wood are of varied breadth; the primary rays may be 8-seriate, e.g. in *Carallia integerrima*, fairly broad also in *Rhizophora Mangle* and *Ceriops Roxburghiana*, only 1–3-seriate in *Cassipourea macrophylla*, DC. The vessels have lumina of various sizes (diameter reaching ·09 mm. in *Carallia*); usually, however, they do not have wide lumina. Scalariform bordered pitting often occurs on the walls by which adjacent vessels touch one another (e.g. *Rhizophora*, *Ceriops*, *Bruguiera*, *Gynotroches*). The wall of the vessel, when in contact with the parenchyma of the medullary rays, bears bordered pits, and sometimes side by side with them simple pits. The wood-parenchyma is not very abundantly developed anywhere, occurring, however, not only in the neighbourhood of the vessels, but also among the wood-fibres.

Regarding the **pith**, it is only necessary to state that in *Rhizophora* this tissue contains the H-shaped spicular cells, which recur also in the primary cortex of the same genus. Of the two arms of these cells, one is generally longer than the other, and in place of the shorter one, a few very short branches are occasionally present.

The structure of the **cortex** has so far been little investigated, namely by Möller in *Rhizophora Mangle* and *R. mucronata*, and by me in the branches of *R. Mangle* and *Carallia integerrima*. The formation of cork is superficial in both genera. The cork of *Rhizophora Mangle* is of the typical spongy form; in *Carallia integerrima* the cork-cells have lumina of less width. In the two species investigated by me, a composite and continuous sclerenchy-

matous ring occurs in the pericycle; in *Carallia* some of the cells of this ring, when seen in transverse section, exhibit sclerosis on one side or in the form of a horseshoe. Even in the older specimens of cortex examined by Möller, secondary hard bast is not present.

4. Structure of the Root. Regarding the interesting root-structure of *Bruguiera caryophyllaeoides* and *Rhizophora Mangle*, both of which, as is well known, possess aerial roots (stilt-roots), the following description is taken from Schimper.

The roots of *Bruguiera* have a thick cortex, which is rich in intercellular spaces; the thickness of the cortex is much less in the parts of the root projecting above the soil than in the subterranean parts. The intercellular spaces form radial slits, and are of schizogenous and lysigenous origin. The cell-layers bounding the intercellular spaces are provided with annular lignified thickening ridges, which serve to strengthen the loose and otherwise thin-walled tissue. It may be pointed out that the intercellular spaces are larger in the subterranean portions of the roots than in the aerial parts, and that the cortex of the latter alone contains stone-cells; further, that in the soil the periderm consists of cork-cells only, while in the air it is composed of alternating layers of cork and parenchymatous separating tissue ('parenchymatische Trennungsgewebe').

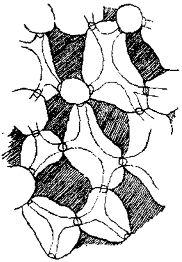

Fig. 75. A portion of a transverse section through the cortex of the root of *Rhizophora Mangle*, L.—After Warming.

The stilt-roots of *Rhizophora* also exhibit a different structure, according to the part examined—whether this is embedded in the mud, or projects above it. The greater thickness of the part of the root which is buried in the soil is, in this case also, connected with the strong development of the primary cortex. In the subterranean parts of the stilt-roots, as in the lateral roots, the structure of which has been thoroughly described by Warming, the primary cortex (Fig. 75) consists of two kinds of cells: firstly, cells which are elongated in the radial direction and are connected with one another tangentially by short lateral arms, and, secondly, cells which are elongated in the vertical direction are arranged in rows, and appear in transverse section as rather small roundish lumina. Only the radially elongated cells are provided with thickening ridges, where they adjoin one another or come in contact with the cells with rounded lumina. The part of the root projecting above the mud has a primary cortex, which is thinner and is traversed by considerably narrower intercellular passages. Into these intercellular spaces project the H-shaped spicular cells, already described above in the leaf and axis; they are almost completely wanting in the subterranean part of the root. Here the cortical parenchyma consists of uniform roundish-polygonal cells without thickening ridges.

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COMBRETACEAE[1].

1. Review of the Anatomical Features. For the anatomical diagnosis of the Order, the following characters may first be pointed out.

[1] The Order is not taken here with quite the same limits as in Bentham and Hooker. The carpeae are excluded and are treated later in the Hernandiaceae (q. v.).

With the single exception of *Macropteranthes*, the vascular bundles are bicollateral in structure, even in *Laguncularia* and *Lumnitzera*, in which the intraxylary soft bast is very much reduced, and is therefore easily overlooked. The wood shows a uniform structure; the vessels, which have lumina of various sizes, have simple perforations throughout, and bear bordered pits even where they are in contact with parenchyma; the medullary rays are for the most part narrow; the groundwork of the wood is almost always formed by wood-prosenchyma with simple pits. In addition to these characters we have the usually bifacial leaf-structure; the lack of mucilaginous epidermal cells; the absence of subsidiary cells accompanying the guard-cells; the excretion of oxalate of lime chiefly in the form of clustered crystals, which frequently give rise to transparent dots in the leaf, and occur in tangentially arranged chambered fibres in the bast of the axis, whilst solitary crystals are rare, and are found almost solely in the lignified tissues of the axis; lastly, the characteristic, unbranched and unicellular, but two-chambered trichomes (Fig. 76, *A–B*), which are present in all the genera of the Order, and will be treated in greater detail in the discussion of the leaf-structure.

In addition to the above, some other anatomical features, concerning the hairy covering and the structure of the axis and leaf, may now be indicated. Side by side with the two-chambered unicellular hairs other trichomes occur, namely long- or short-stalked glandular hairs (*Calycopteris, Guiera, Combretum, Thiloa, Cacoucia, Quisqualis* and *Laguncularia*), the latter often of small scale-like shape; and in one case (*Conocarpus*) two-armed unicellular trichomes are also found. The origin of the cork is mostly internal, more rarely (*Terminalia* pro parte, *Lumnitzera, Laguncularia* and *Macropteranthes*) superficial. In the pericycle isolated bundles of hard bast are sometimes present; on the inner side of the groups of hard bast a broad parenchymatous pericycle is occasionally developed. Secondary hard bast has been observed in the Order. In *Calycopteris, Guiera* and *Thiloa*, as well as in many but not all of the African species of *Combretum*, the xylem contains interxylary phloem. Other special features of the leaf and axis are: formation of papillae on the lower epidermis of the leaf (species of *Combretum*); development of hypoderm on the upper side of the leaf (*Combretum ternatum*, Wall.); sclerenchyma-fibres, running free in the mesophyll (species of *Terminalia, Ramatuella, Anogeissus, Combretum* and *Thiloa*); intercellular mucilage-receptacles in the veins of the leaf, in the medullary sheath and in the wood of the branches (species of *Terminalia*); crystal-sclerenchyma (*Macropteranthes*).

2. Structure of the Leaf[1]. The **leaf-structure** is mostly bifacial, rarely centric. In the centrically constructed leaves of the species of *Laguncularia*, the middle of the leaf is occupied by aqueous tissue, which is adjoined on both sides by palisade-tissue.

The large **leaf-veins** have a vascular bundle-system of bicollateral structure; the bundle-system is either enclosed by a ring or arc of sclerenchyma (species of *Terminalia, Conocarpus, Ramatuella, Anogeissus, Guiera, Macropteranthes, Combretum, Thiloa, Cacoucia* and *Quisqualis*), or is only accompanied by a few sclerenchyma-fibres (species of *Terminalia, Calycopteris, Macropteranthes* and *Combretum*), while in certain species of *Terminalia, Lumnitzera* and *Combretum* the sclerenchyma is wanting. The vascular bundles of the smaller veins are either embedded (species of *Terminalia, Conocarpus, Ramatuella, Anogeissus, Lumnitzera, Laguncularia, Combretum, Thiloa*) or vertically transcurrent. Sclerenchyma accompanies them in large or small amount

[1] The following description is based essentially on the work of Heiden (Bot. Centralbl., 1893), who investigated nearly ninety species, belonging to all the twelve genera.

(species of *Terminalia*, *Ramatuella*, *Anogeissus*, *Guiera*, *Macropteranthes*, *Combretum*, *Thiloa*, *Cacoucia*, *Quisqualis*), or is absent (species of *Terminalia*, *Calycopteris*, *Anogeissus*, *Lumnitzera*, *Macropteranthes*, *Laguncularia* and *Combretum*). In the vertically transcurrent veins sclerenchyma (species of *Terminalia*, *Calycopteris*, *Anogeissus*, *Combretum*, *Thiloa* and *Quisqualis*) or thin-walled strengthening tissue (species of *Terminalia*, *Anogeissus*, *Guiera* and *Combretum*) extends from the vascular system to the epidermis of each surface. In certain members of the Order[1], sclerenchyma-fibres branch off from the veins and run freely and on the whole quite irregularly in the mesophyll, as well as between the epidermis and the subjacent leaf-parenchyma.

The following special points may be mentioned regarding the **epidermis** of the leaf. The lateral walls of the epidermal cells are either undulated or straight. In *Combretum lanceolatum*, Pohl, the epidermal cells on the lower side are subpapillose or papillose; in *C. Aubletii*, DC. they possess mammilliform papillae. The walls of the epidermal cells are usually not much thickened. Marginal pits are present in *Combretum acuminatum*, Roxb., *C. capituliflorum*, Fenzl., *C. Jacquini*, Griseb. and *C. laurifolium*, Mart., as well as in *Ramatuella*. Strong markings on the cuticle are wanting; delicate striation of the latter has been observed only in some species of *Combretum*. It should be noticed that Heiden did not meet with gelatinization of the epidermis in any of the numerous members of the Order investigated by him. Hypoderm has been observed below the upper epidermis of the leaf only in *Combretum ternatum*, Wall., where it is developed as a single layer and only locally. The guard-cells of the **stomata** are not accompanied by any special subsidiary cells. The stomata are, as a rule, found only on the lower surface of the leaf; they also occur on the upper side in *Terminalia crenulata*, Roth., *Conocarpus*, *Guiera*, *Lumnitzera*, *Macropteranthes montana*, F. v. Müll., *Laguncularia*, *Combretum altum*, Guill. et Perr., *C. nanum*, Ham. and *C. trichanthum*, Fres. var.

As regards the **hairy covering**, two principal types can be distinguished in the Order, namely (1) simple, unicellular hairs, in addition to which unicellular, two-armed hairs are present in one genus (*Conocarpus*), and (2) glandular hairs. The simple, unicellular hairs have a very general distribution in the Order. Their peculiar feature (Fig. 76, *A–B*) consists in the fact that the base of the hair, which is usually somewhat swollen in a bulbous manner, is bounded towards the filiform principal part of the hair by a cellulose membrane, more or less convexly or conically arched outwards towards the filamentous portion. Thus it often appears as if the hairs in question were bicellular; the base seems to consist of a cell, which is blunt or drawn out into a long point at its end, and has its upper end apparently inserted in a filiform hair-cell. Heiden has proved by a developmental investigation that these hairs are actually unicellular and not bicellular. The simple hairs vary in length, in the thickness of their walls and in the width of their lumina[2]. Regarding the unicellular two-armed hairs, which have already been mentioned in *Conocarpus* (Fig. 76, *C*), it may be added that the stalk, which forms part of the single cell, is short, and that the terminal portion has equal arms. Transitions to these two-armed trichomes are formed by the

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[1] These are *Bucida Buceras*, L., *Buchenavia ochroprumna*, Eichl.; *Ramatuella argentea*, H. B. K., *R. virens*, Spruce; *Anogeissus acuminata*, Wall., *A. leiocarpa*, Guill. et Perr.; *Combretum acuminatum*, Roxb., *C. Aubletii*, DC., *C. decandrum*, Roxb., *C. elegans*, Camb., *C. Jacquini*, Griseb. var. *laurifolium*, Mart., *C. Monetaria*, Mart., *C. nitidum*, Spruce, *C. obtusifolium*, Rich., *C. phaeocarpum*, Mart.; *Thiloa glaucocarpa*, Eichl., *T. gracilis*, Eichl., *T. stigmaria*, Eichl. In *C. salicifolium*, E. Mey., they are absent, contrary to a statement of Holtermann's on the subject.

[2] Quite analogous trichomes, it may be noted, have also been observed in the Cistineae (q. v.).

one-armed hairs in some species of *Terminalia* (Fig. 76, *D*) and in *Ramatuella*. The latter have a small stalk sunk in the epidermis, are more or less adpressed to the surface of the leaf, and have a fully developed arm on one side only, whilst on the other there is only a short protrusion ; the cellulose membrane is present in the basal portion, as in the ordinary hairs.

The glandular hairs are of various shapes, and are always composed of fairly numerous cells. To begin with, they may be subdivided into ; firstly, shortly stalked or almost sessile glandular hairs, with a spherical or disc-shaped

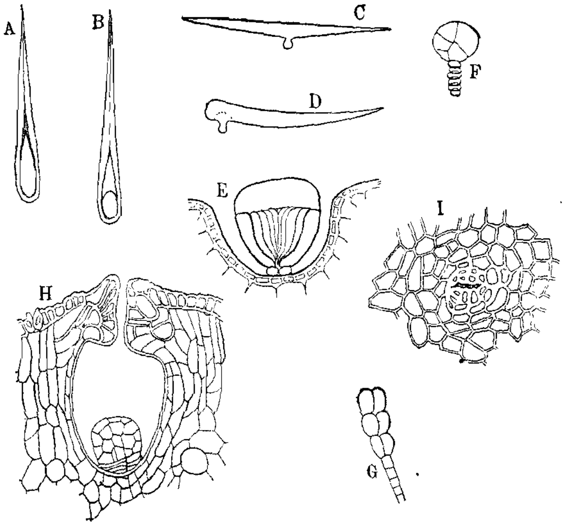

FIG. 76. A, B, Ordinary Combretaceous hairs. C, Two-armed hair of *Conocarpus*. D. One-armed hair of *Terminalia argentea*, Mart. E, Glandular hair of *Calycopteris* in section. F, External gland of *Combretum aculeatum*, Vent. G, External gland of *Combretum decandrum*, Roxb. H, I, Glandular leaf-pit of *Laguncularia racemosa*, Gärtn. f.—A, G after Heiden ; H, I, after Holtermann.

head, which consists of a single layer of radially arranged cells ; and secondly, glandular hairs, with a more or less considerably elongated stalk, and a spherical or ellipsoid head composed of many or few cells, always showing irregular arrangement, and never forming a cell-surface. In one case, the glandular hairs of the first type are bladder-like integumental glands, the secretion being excreted between a cup-shaped cell-surface and the cuticle ; the head of the gland is spherical, and the structure of the plate of cells is difficult to recognize from above, on account of the accumulation of secretion (*Calycopteris*, Fig. 76 *E*, *Guiera*, *Combretum* pro parte). In another case we have small glandular scales, the accumulation of secretion beneath the cuticle being

slight or wanting; in consequence of this the structure of the plate of cells is distinct when seen from above (*Thiloa, Combretum* pro parte). The plate of cells presents a varied appearance in surface-view, inasmuch as the scale is either formed by ray-cells all of which meet at the centre of the shield, or by ray-cells extending inwards from the margin and only in part reaching the centre, or lastly, by ray-cells, some or all of which are divided by tangential walls. This diverse structure of the scale is of value for the diagnosis of species, as O. Bachmann and Heiden have shown in detail; but at the same time it must be taken into consideration that several of the above-described types of structure of the shield are occasionally met with side by side in one and the same species. The glandular hairs of the second type include the external glands of those species of *Combretum* which previously constituted the genus *Poivrea*, of *Quisqualis* and *Cacoucia*. They either have a spherical (Fig. 76, *F*) or an ellipsoidal (Fig. 76, *G*) head; both forms of head are occasionally to be found side by side in the same species. The glandular hairs of *Cacoucia* are characterized by a specially long multicellular stalk; they are adpressed to the leaf-surface in consequence of a curvature of the stalk near its base. Quite a special form of external gland is to be met with in *Laguncularia racemosa*, Gaertn. (Fig. 76, *H–I*). This has a cap-like shape, and possesses a very short, scarcely developed stalk, consisting of several rows of cells; attached to the stalk is a glandular head, which consists of polygonal, irregularly arranged cells, and is almost of the same breadth as the stalk, so that it is scarcely delimited from it. These glands occur singly at the bottom of extremely characteristic pits, which are found on both sides of the leaf, are fairly deep, and have a flask-like shape, and a narrow slit-like canal opening externally. Holtermann met with similar pits on the lower side of the leaf of *Conocarpus erectus*, L.; these are, however, without glandular hairs, as they are replaced by the cells of the wall, which exude a secretion; in this case the pits occur only in the angles between the principal vein and the larger lateral veins.

In connexion with the glandular hairs, mention may be made of the relatively large petiolar glands, recognizable even with the naked eye, and described by Bentham and Hooker as occurring in species of *Terminalia, Conocarpus, Anogeissus* and *Laguncularia*. In *Laguncularia racemosa*, according to Höhnel (Bot. Zeit., 1882) they contain a small-celled glandular tissue.

In the leaf **oxalate of lime** occurs almost exclusively in the form of clustered crystals. Transitions to solitary crystals were met with by Heiden in *Combretum pilosum*, Roxb. only, true solitary crystals (together with clustered crystals) in *Terminalia citrina*, Roxb. Other forms of excretion of oxalate of lime are wanting. In the leaf the clustered crystals occur both in the mesophyll and accompanying the vascular bundles of the veins. Those of the palisade-tissue are frequently of considerable size, and are contained in correspondingly large idioblasts, which often penetrate deep into the spongy parenchyma, and in some cases traverse the entire mesophyll. Large idioblasts of this kind, bearing clustered crystals, are found in species of *Terminalia, Conocarpus, Anogeissus, Guiera, Macropteranthes, Laguncularia, Combretum, Thiloa* and *Quisqualis*, and, when the thickness of the leaf is not too great, give rise to well-marked transparent dots (see Bokorny and Heiden, loc. cit.). Regarding the size of the clustered crystals, we may add that their diameter occasionally reaches ·13 mm.; and, with respect to their form, that they are either differentiated in the shape of a regular star, or, owing to stronger development of one or more of the individual crystals, a star with unequal rays.

Of internal **secretory organs** the secretory cavities, which are elongated after the manner of canals, and are filled with mucilaginous contents, alone

require special mention; they occur in *Terminalia Arjuna*, Bedd., *T. crenulata*, Roth., *T. pellucida* Presl., and *T. tomentosa*, W. et A., above the xylem of the veins, and thence occasionally penetrate into the mesophyll. They have a distinct epithelium, and a fairly large diameter (reaching ·175 mm.). Fatty bodies also are further frequently met with in the assimilatory tissue (Radlkofer).

3. STRUCTURE OF THE AXIS. The structure of the **cortex** has been investigated by Holtermann, Brandis, and especially by Heiden in extension of the earlier statements of J. Möller.

The formation of cork is either superficial or internal. Superficial development of cork is found in a certain number of the species of *Terminalia* and in the investigated species of *Lumnitzera* and *Laguncularia*, where the subepidermal cell-layer becomes the phellogen, as well as in *Macropteranthes*, where the second or third cell-layer of the primary cortex from the outside produces the cork; internal cork-formation, on the other hand, occurs in another series of species of *Terminalia*, and in the investigated species of *Calycopteris, Conocarpus, Ramatuella, Anogeissus, Guiera, Combretum, Thiloa, Cacoucia* and *Quisqualis*. In the last-named genera the phellogen nearly always arises immediately on the inner side of the pericyclic bundles of sclerenchyma-fibres, in the outermost part of the often broad parenchymatous pericycle. In *Ramatuella*, in which the pericyclic groups of fibres are wanting, the cork appears to be developed in the middle of the primary cortex, unless the parenchyma, occurring on the inner side of the cork, and having the appearance of ground-tissue, is to be regarded as a parenchymatous pericycle. The cork-cells mostly have wide lumina and thin walls; sometimes, however, cells sclerosed on one side, or stone-cells are also present in the cork. In *Quisqualis* the cork-cells are strongly elongated in the radial direction; according to Heiden, the radial elongation in this case only takes place subsequently, after the cells derived from the phellogen have already been suberized.

There is little to be said respecting the primary cortex. Stone-cells only occasionally occur in it, but clustered crystals are frequently found, while solitary crystals have only been observed by Holtermann in *Combretum decandrum*, Roxb. and *C. extensum*, Roxb. The pericycle ordinarily shows sclerenchymatous development in its outer part in the form of isolated groups of sclerenchyma-fibres. The latter are commonly adjoined internally by a broad parenchymatous ring of pericycle. In *Terminalia dichotoma*, E. Mey. and *T. Tanibouca*, Sm., the walls of the pericyclic sclerenchyma-fibres may ultimately undergo solution (Heiden). In *Ramatuella*, as has been mentioned above, the pericyclic groups of sclerenchyma are wanting.

In many members of the Order the secondary bast contains small islands or bands of secondary hard bast. A very characteristic feature of the secondary bast is the presence of chambered crystal-fibres, which have their chambers occupied by small clustered crystals, and are arranged in tangential bands in the transverse section of the branch (in species of *Terminalia, Conocarpus, Anogeissus, Lumnitzera, Laguncularia, Combretum, Thiloa, Quisqualis*). The crystal-sclerenchyma of *Macropteranthes* constitutes an isolated feature. In this genus groups of stone-cells occur in the pericycle or in the bast as well; the cell-walls of the stone-cells are only in some cases slightly thickened, while the lumen of these elements is filled by a solitary crystal.

Intraxylary phloem has been demonstrated by various observers (Höhnel, Petersen, Solereder, Holtermann, Heiden) in numerous species of the genera *Terminalia, Calycopteris, Conocarpus, Ramatuella, Anogeissus, Guiera, Combretum, Thiloa, Cacoucia* and *Quisqualis*, and also in the recently established genus *Pteleopsis* (*P. variifolia*, Engl.). It is wanting in *Macropteranthes* only

(Heiden). In *Laguncularia* and *Lumnitzera*[1] it is easily overlooked, as it is only present in the form of few-celled groups of tissue at the periphery of the pith. The intraxylary phloem either forms a ring or separate strands of tissue at the outer margin of the pith. After renewed investigation I am unable to confirm Holtermann's statement, that small groups of soft bast occur scattered in the pith of *Conocarpus erectus*, L. In some cases the development of the inner soft bast is quite considerable, and is then increased by the activity of a cambial zone, lying between the wood and the inner soft bast; under these circumstances the portions of phloem directed towards the pith are often compressed like horn-bast. Finally, it remains to be mentioned that the soft bast is occasionally strengthened at its inner margin by sclerenchymatous cells.

The **pith** for the most part consists of lignified and fairly thick-walled cells, more rarely of unlignified, thin-walled cells. Groups of stone-cells occur in considerable numbers in the pith, e. g. of *Calycopteris*; in *Terminalia fagifolia*, Mart., almost the whole of the pith consists of stone-cells. In some species of *Combretum* (*C. acuminatum*, Roxb., *C. collinum*, Fres., *C. extensum*, Roxb., *C. squamosum*, Roxb.), prosenchymatous or parenchymatous sclerenchyma-cells, elongated in the vertical direction, are met with in the pith; their relatively wide lumina are filled with a white substance, the nature of which is not known (not silica). Secretory canals, filled with mucilage, are present in the medullary sheath of some species of *Terminalia* (*T. Arjuna*, Bedd., *T. Bellerica*, Roxb., *T. Catappa*, L., *T. crenulata*, Roth., *T. paniculata*, Roth., *T. procera*, Roxb., *T. tomentosa*, W. et A.). As Höhnel was the first to show, the development of these canals is schizogenous.

The structure of the **wood** has been investigated by J. Möller, Solereder, Heiden and Holtermann. The medullary rays are mostly narrow, being broader in the twining species only (5-seriate in *Quisqualis*, according to Holtermann). Tier-like differentiation of the medullary rays has been observed by Höhnel in the wood of the stem of a Combretaceous plant described as '*Conocarpus erecta ?*' In a transverse section the vessels are isolated, or a few of them are grouped together in a radial direction; in certain species the lumen of the vessels is very small, but in the lianes very wide. The perforations are simple, and, in the vessels with wide lumina, occur on horizontal division-walls, which are resorbed so as to leave only a narrow annular ridge. The walls of the vessels are provided with bordered pits, even where they are in contact with the parenchyma of the medullary rays; Holtermann, however, mentions having also observed simple pitting (?) on these areas. Spiral thickening of the walls of the pitted vessels has not been demonstrated anywhere. The bordered pits on the walls of the vessels are characterized by the sieve-like structure of the pit-membrane, first observed by Bengt Jönsson. The wood-prosenchyma, which is variously differentiated as regards thickness of walls and size of lumina, bears simple pits, or the pits are at the most only provided with a very narrow and indistinct border. According to Holtermann, an exception is afforded by *Combretum decandrum*, Roxb., in which the groundwork of the wood is stated to consist of fibrous tracheides. The simple-pitted prosenchyma is sometimes septate by means of a few delicate division-walls (species of *Anogeissus*, *Combretum*, *Cacoucia*, *Quisqualis*, *Guiera*, *Conocarpus*, *Terminalia* and *Calycopteris*), and in such cases occasionally contains solitary crystals (species of *Combretum* and *Terminalia*). The wood-parenchyma is usually restricted to the neighbourhood of the vessels; more rarely (*Terminalia Bellerica*, Roxb.) it traverses the wood-prosenchyma in the form of tangential bands. In some species of *Terminalia* chambered crystal-parenchyma has

[1] Holtermann was able to demonstrate internal soft bast in alcohol-material of *Lumnitzera*.

been observed. Unlignified wood-parenchyma has been met with in the twining plant *Quisqualis indica*, L. (Witte).

To conclude the description of the structure of the wood, the occurrence of secretory spaces in the **xylem**, and of interxylary phloem remain to be considered. The secretory spaces, which Heiden met with in relatively thick portions of the branches of *Terminalia Bellerica*, Roxb. and *T. macroptera*, Mart., have yellowish contents, giving a mucilage-reaction, and apparently the result of disorganization of woody tissue. Interxylary phloem is present in a certain number of the African species of *Combretum*, in *Calycopteris*, *Guiera* and *Thiloa*. The islands of soft bast in the wood are relatively large, and are arranged in concentric circles. They include no bast-fibres, but frequently contain numerous clustered crystals. With regard to their origin, they are given off externally by the cambium in *Guiera* (according to Chodat), and *Calycopteris* (according to Heiden), i. e. as in *Strychnos*; on the other hand, in the plant described by Holtermann as *Combretum salicifolium*, E. Mey.[1], they are produced internally by the cambium.

Interxylary phloem has already been described in my 'Holzstruktur' in the three genera *Calycopteris* (*C. floribunda*, Lam.), *Guiera* (*G. senegalensis*, Lam.) and *Thiloa* (*T. glaucocarpa*, Eichl., *T. gracilis*, Eichl. and *T. stigmaria*, Eichl.). To these we must add, according to Holtermann, the South African *Combretum salicifolium* already mentioned; but not, as H. Schenck states, some 'Indian species of *Combretum*,' the names of which are not given. Holtermann's statement induced me to investigate the species of *Combretum* present in the Herbar. Monac. at the time, with regard to the occurrence or absence of interxylary phloem. The result was the demonstration of its occurrence in a certain number of the African species, namely, in *Combretum erythrophyllum*, Sond., *C. Hartmannianum*, Schweinf., *C. Kraussii*, Hochst., *C. lepidotum*, Rich., *C. Nyikae*, Engl., *C. Rueppellianum*, Rich., *C. salicifolium*, E. Mey., *C. Schelei*, Engl., *C. tenuispicatum*, Engl., *C. trichanthum*, Fres. It still remains to be determined whether these species form definite groups of affinity, or whether interxylary phloem appears in the other species, but only in the later growth of the wood.

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MYRTACEAE.

1. Review of the Anatomical Features. The Order of the Myrtaceae, in the sense of Bentham and Hooker, Gen. plant., does not constitute a single group of affinity either as regards anatomical or exomorphic characters. The Order must be divided into two sections, which may either be called Suborders or Orders; the latter course has been adopted in the

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[1] I am inclined to doubt the correct determination of this plant, as Holtermann describes and figures sclerenchyma-fibres running irregularly in the mesophyll, and these do not occur in *C. salicifolium*, E. Mey. The true *C. salicifolium*, E. Mey., however, also possesses interxylary soft bast.

'Natürliche Pflanzenfamilien.' The first section includes the three tribes Chamaelaucieae, Leptospermeae and Myrteae, and will, in the following description, be comprised under the name 'Myrtaceae sensu strictiore'; the second section consists of the genera of the three other tribes—the Lecythideae, Barringtonieae, and Napoleoneae (or Belvisieae), and will be designated by the name Lecythidaceae.

The Myrtaceae sens. str. are characterized by the occurrence of schizogenous secretory cavities, which very frequently cause a transparent dotting of the leaves; by the possession of intraxylary phloem; and by the bordered pitting of the wood-prosenchyma. In the Lecythidaceae, on the other hand, the secretory cavities are wanting, as is also the intraxylary phloem; the wood-prosenchyma bears simple pits; a special character of the Lecythidaceae consists in the occurrence of cortical vascular bundles. With regard to the cortical bundles of the Lecythidaceae, it may be added that the three tribes may be distinguished by the fact that these bundles are inversely orientated (i. e. with bast inwards and wood outwards) in the Barringtonieae, normally orientated (i. e. with bast outwards and wood inwards) in the Lecythideae and Napoleoneae, and that the number of the cortical bundles amounts to four in the Napoleoneae, to more than eight in the Lecythideae.

Apart from these important characters, which enable us at once to distinguish the Myrtaceae sens. str. from the Lecythidaceae, some other anatomical features are common to both sections. All the Myrtaceae have narrow medullary rays in the wood. The abundance of tannin in all the Myrtaceae is noteworthy. Oxalate of lime is excreted only in the form of ordinary solitary or clustered crystals. The hairy covering is of a simple type, and consists almost solely of unicellular or uniseriate clothing hairs; glandular hairs are extremely rare; semi-malpighian or malpighian unicellular trichomes have been observed in *Myrcia* and *Calyptranthes*. A characteristic type of stoma is common neither to the Myrtaceae in general nor to the members of either of the two subdivisions; for the stomata are either surrounded in an irregular manner by three or more epidermal cells of no distinctive shape, or are accompanied by subsidiary cells, which are parallel to the pore; and these features vary from genus to genus. The same holds good for the origin of the cork; this tissue is either developed subepidermally or at a varying depth in the primary cortex, or in the pericycle immediately internal to the primary hard bast. The perforations of the vessels are either simple or scalariform. Stratification of the bast into hard and soft zones is very widely distributed in the Order. It is only wanting in the genera of the Chamaelaucieae.

Special anatomical characters, which are of importance only for detailed diagnosis, are as follows: papillose differentiation of the lower epidermis of the leaf (species of *Melaleuca, Couratari, Lecythis*); occurrence of hypoderm on the upper side of the leaf (species of *Psidium* and *Metrosideros*); occurrence of an excretion of wax on the surface of the vegetative organs (*Eucalyptus*); cork-warts on the lower side of the leaf (*Acmena, Eucalyptus*); sclerenchyma-fibres running irregularly in the mesophyll (*Jambosa vulgaris*, DC., *Asteranthos brasiliensis*, Desf.); gum-canals in the pith (certain species of *Bertholletia, Couratari, Lecythis*).

Finally, the 'genera anomala' appended to the tribe Napoleoneae (Belvisieae) in Durand's Index may now be briefly considered. Only a few of these have been anatomically investigated. In *Foetidia* the secretory cavities and the intraxylary phloem are wanting; on the other hand, cortical vascular bundles occur, and *Foetidia* must therefore be included amongst the Lecythidaceae, to which recent systematists have also referred it. Costantin and Dufour state that in the structure of its branches the genus *Catostemma* agrees neither with the Lecythideae nor with the Ternstroemiaceae. According to the same authors, the

anomalous genus *Cupheanthus* has no secretory cavities but possesses intraxylary soft bast. The genus *Fropiera*, in which secretory cavities will probably be found, as suggested by the statement 'folia pellucido-punctata,' as well as the remaining anomalous genera, may be recommended for anatomical investigation; the anatomical method will certainly be able to throw light on their affinities. The genus *Petersia* is likewise worthy of more detailed anatomical investigation; it is generally referred to the Lecythidaceae (Barringtonieae), but, according to Niedenzu, cortical vascular bundles are wanting; secretory cavities, however, probably occur ('folia pellucido-punctata!' according to Bentham and Hooker).

A. Myrtaceae sens. str.

(Tribes Chamaelaucieae, Leptospermeae, Myrteae.)

2 A. Structure of the Leaf[1]. In the Myrtaceae sens. str. the **mesophyll** very frequently has centric structure, e.g. in the vertically placed leaves of *Callistemon linearis*, and in the cylindrical leaves of *Calothamnus*. In the last-named genus, aqueous tissue occupies the middle of the leaf. Bifacial leaf-structure occurs, e.g. in *Acmena floribunda*, *Eucalyptus globulus*, *E. pilularis* and *E. gomphocephala*; these species have both vertical and horizontal leaves, which mostly differ from one another in their form, and also exhibit dimorphism in the structure of the leaf, the vertically placed leaves being centric in structure, the horizontal leaves bifacial. It is, however, not intended to imply that in *Eucalyptus* centric structure is invariably connected with vertical position of the leaves. The horizontal and vertical leaves of two species, described by Leclerc du Sablon as *E. jugalis* and *E. fallax*, are equally centric in structure. The **stomata** are either accompanied by no special subsidiary cells or by two such cells parallel to the pore (*Myrcia*). It goes without saying that in leaves with centric structure the stomata are found on both sides. In certain species of *Eucalyptus* (*E. globulus* and *E. pulverulenta*) the outer wall of the **epidermis** is provided with a coating of wax; the latter consists of an aggregate of small rod-like particles. In some cases hypoderm occurs beneath the upper epidermis of the leaf; e.g. according to Bokorny in *Psidium Araca*, Raddi and *P. incanescens*, Mart., and according to Diels in *Metrosideros robusta*, A. Cunn. and *M. tomentosa*, A. Cunn. *Melaleuca hypericifolia* shows papillose differentiation of the lower epidermis of the leaf. In *Jambosa vulgaris* sclerenchyma-fibres, having an irregular course, are present in the mesophyll. The **hairy covering** of the Myrtaceae sens. str. usually consists of simple unicellular hairs; unicellular one-armed hairs have been met with in *Myrcia rostrata*, DC., unicellular two-armed hairs with unequal arms in *M. itambensis*, Berg, unicellular two-armed hairs with arms of equal length in *Calyptranthes mutabilis*, Berg; glandular hairs are wanting. Cork-warts, resembling lenticels, have been observed on the leaves of *Eucalyptus calophylla*, *E. globulus*, *E. Gunnii*, *E. megacarpa*, *E. obliqua* and *E. siderophloia*, as well as in *Acmena floribunda*.

Oxalate of lime occurs only in the form of clustered and ordinary solitary crystals. The mesophyll is characterized by the abundance of tannin.

The **secretory cavities** form the most characteristic anatomical feature. They occur not only in the leaf, but also in the ground-tissue of the axis. In the leaf they very frequently give rise to transparent dots. The secretory

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[1] The following statements as to the structure of the leaf and axis of the Myrtaceae sens. str. are essentially based on Lignier's treatise in the Arch. bot. du Nord de la France. Numerous species of the genera *Darwinia*, *Verticordia*, *Chamaelaucium*, *Baeckea*, *Leptospermum*, *Callistemon*, *Melaleuca*, *Calothamnus*, *Eucalyptus*, *Tristania*, *Metrosideros*, *Psidium*, *Myrtus*, *Myrcia*, and *Eugenia* (sensu Durand) were investigated by Lignier.

cavities in question are present in all Myrtaceae sens. str., as may be concluded from the statements in the literature. In a very large number of the genera anatomical proof of the occurrence of secretory cavities has been obtained, especially through the investigations of Bokorny[1]; in the remaining genera the presence of secretory cavities may be inferred, since pellucid dots are described by systematists as occurring in their leaves. The secretory cavities are schizogenous in origin, as Frank, Höhnel, Bokorny, Van Tieghem, and Leblois have shown, contrary to the statements of Martinet and Chatin. In correspondence with their mode of origin they are lined with a distinct epithelium. From the most recent developmental investigation of these cavities by Lutz, which likewise confirms their schizogenous origin, one gathers that in the leaf they are almost always developed at a very early stage by division of one or of two epidermal cells; further, that the secretion is not formed in the lumen of the epithelial cells, but in that wall of the secreting cells ('resinogenous layer'), which is arched outwards towards the secretory space; and lastly, that the epithelial cells are obliterated at an early stage, i.e. become compressed and often suberized. In the mature leaf the secretory cavities occur beneath the epidermis, usually on both sides of the leaf. The

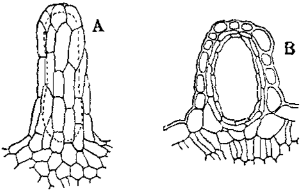

FIG. 77. A, B, Secretory cavity in an emergence of the leaf of *Eucalyptus citriodora*.—After Lignier.

axis always contains these cavities in the primary cortex, rarely (*Tristania macrophylla*) in the pith[2] also. The species *Eucalyptus citriodora*, which is characterized by possessing leaves of two different forms, is specially noteworthy, owing to the fact that in the long narrow leaves and in the branch the secretory cavities are enclosed in hair-like emergences of cylindrical shape, rounded at the end, and of epidermal origin (Fig. 77, *A–B*). In the root the secretory cavities are wanting (Van Tieghem). The contents of the cavities are almost always of an oily nature. According to Lutz, *Tristania laurina* alone forms an exception in this respect; in this species the secretory cavities, which are also provided with a distinct epithelium, though they are not derived solely from the epidermis, contain a mucilaginous substance.

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[1] Bokorny's researches extend to numerous species of the following genera: Tribe Chamaelauciese: *Actinodium*, *Darwinia*, *Homoranthus*, *Verticordia*, *Chamaelaucium*, *Calythrix*, *Lhotzkya*, *Thryptomene*; Tribe Leptospermeae: *Baeckea*, *Astartea*, *Hypocalymma*, *Agonis*, *Leptospermum*, *Kunzea*, *Callistemon*, *Melaleuca*, *Beaufortia*, *Regelia*, *Calothamnus*, *Eremaea*, *Angophora*, *Eucalyptus*, *Tristania*, *Metrosideros*; Tribe Myrteae: *Campomanesia*, *Psidium*, *Psidiopsis*, *Rhodomyrtus*, *Myrtus*, *Rhodamnia*, *Decaspermum*, *Myrcia*, *Marlieria*, *Calyptranthes*, *Pimenta*, *Eugenia*, *Calycorectes*. The genera in this enumeration are limited in the same way as in Durand's Index.

[2] The improbable statement of Möller's (Rindenanatomie, pp. 344 and 347) as to the occurrence of resin-spaces in the secondary bast in *Eucalyptus viminalis*, Labill. and *E. Stuartiana*, F. v. Müll. requires re-examination. According to Möller 'spherical (·12 mm. diam.), apparently lysigenous resin-spaces' occur in the first-named species.

With regard to the structure of the **petiole**, it may be remarked that, according to Lignier, in the Myrtaceae sens. str. a single vascular strand passes into the petiole from the axis. In its further course the vascular system of the petiole, as seen in transverse section, either exhibits only one arc of vascular bundles or, in addition to this, two further groups of bundles situated opposite the arc, and symmetrically arranged. The vascular bundles of the petiole, like those of the axis, are bicollateral in structure.

3 A. Structure of the Axis. We have already pointed out the presence of **vascular bundles** with bicollateral structure as characterizing the Myrtaceae in the narrower sense. It is true that so far only a small fraction of the Myrtaceous genera[1] has been examined by the various authors (De Bary, Petersen, Costatin and Dufour, Solereder, Lignier), with respect to the feature in question. Yet in accordance with the experience gained in the detailed investigation of other Orders which are likewise characterized by intraxylary phloem, one may assume that the anatomical character in question belongs quite generally to the Myrtaceae sens. str. The intraxylary phloem is often supported by groups of bast-fibres; occasionally it also undergoes secondary growth in thickness (e.g. in *Eugenia Michelii*, according to Petersen).

Regarding the anatomy of the **wood**, the following account is based on the statements in my 'Holzstruktur,' and in Lignier's treatise. The Myrtaceae have vessels with relatively small lumina, which have either simple or exclusively scalariform (*Eugenia apiculata*, DC., according to Reiche) perforations. The vessel-walls, even where they are in contact with parenchyma, usually bear bordered pits; at these places transitions to simple pitting have been observed in *Eucalyptus Globulus*, Labill. The medullary rays of the wood are narrow, 1–3-seriate. Wood-parenchyma is often only present in a very subordinate amount, but in *Myrtus communis*, L. and *Calycolpus Goetheanus*, Berg, for example, more abundant wood-parenchyma has been met with. The wood-prosenchyma mostly has thick walls, and in the species investigated by me (belonging to the genera *Chamaelaucium, Calythrix, Leptospermum, Eucalyptus, Calycolpus, Myrtus*) bears bordered pits. The pit-borders are, however, occasionally rather small, and the bordered pits are often few in number.

With regard to the structural features of the **cortex**, it may in the first place be pointed out that the place of origin of the cork in the Myrtaceae sens. str. is variable. The investigations undertaken up to the present time, however, lead to the conclusion that this feature is of value for the diagnosis of genera or sub-genera. In some of the species (in *Syzygium Jambolanum, Jambosa densiflora, J. Korthalsii*, and *J. vulgaris*, according to Lignier), the cork arises subepidermally. In other species (*Eucalyptus rostrata, E. robusta, Calothamnus quadrifidus*, species of *Callistemon, Melaleuca ericifolia, M. Preissiana*, and *M. uncinata*, according to Lignier, and *Eugenia australis*, Wendl., according to Möller), a more or less deeply situated layer of the primary cortical parenchyma becomes the phellogen. In a third case the first cork-layer arises in the pericycle; the cell-layer immediately internal to the primary hard bast becomes the cork-cambium. This type includes the following species, according to Lignier: *Leptospermum flexuosum, L. marginatum, Melaleuca styphelioides, M. hypericifolia, Fabricia laevigata, Eugenia, Myrtus*, and *Psidium*, as well as the genera *Darwinia, Chamaelaucium*, and *Verticordia*, belonging to the Chamaelaucieae; according to Möller: *Eugenia acris*, Wight et Arn., *Myrtus communis*, L., *Callistemon lanceolatus*, DC., and *Melaleuca ericifolia*,

[1] These are the following: Tribe Chamaelaucieae: *Actinodium, Darwinia, Verticordia, Chamaelaucium, Calythrix, Thryptomene, Micromyrtus*; Tribe Leptospermeae: *Leptospermum, Callistemon, Melaleuca, Eucalyptus, Tristania, Metrosideros*; Tribe Myrteae: *Psidium, Calycolpus, Myrtus, Myrcia, Myrrhinium, Eugenia.*

Smith. The cork in some cases (in *Syzygium Jambolanum*, DC. and *Eucalyptus rostrata*, Schlecht.) is of the nature of spongy cork, i. e. is composed of cubical cells with delicate walls. In most cases, however, the cork is stratified, layers of thin-walled cells, which are mostly elongated in the radial direction, alternating with layers of cells which are flattened in the radial direction, and are sclerosed on their inner or outer or on both tangential walls. The thin-walled cork-cells of the stratified periderm occasionally show dark Caspary's dots on the radial walls (e.g. in *Melaleuca*). The occurrence of secretory cavities in the primary cortex has already been discussed above. Oxalate of lime occurs in the primary cortex in the form of clustered or ordinary solitary crystals. Stone-cells are present (Lignier) in the primary cortex, e. g. in *Metrosideros tomentosa*. The outer limit of the bast in the Myrtaceae sens. str. is formed by a more or less continuous mechanical sheath of groups of primary bast-fibres. The secondary bast is usually stratified, consisting of alternating layers of hard and soft bast. According to Lignier, an exception to this is afforded by the genera *Darwinia*, *Chamaelaucium*, and *Verticordia*, belonging to the Chamaelaucieae, in which bast-fibres are wanting in the secondary bast, as well as by the genus *Myrtus*, in which only a few rod-cells (sclerosed parenchyma-cells) are developed in the soft bast. According to Möller, stone-cells occur in the secondary bast in *Syzygium Jambolanum*, DC., and species of *Eucalyptus*; the stone-cells attain considerable dimensions in the species of *Syzygium* mentioned, and in *Eucalyptus corymbosa*, Sm., while in other species of *Eucalyptus* they are only slightly sclerosed. Oxalate of lime is present in the bast in the form of clustered or solitary crystals. According to Möller, chambered fibres occupied by solitary crystals occur in species of *Melaleuca*, *Callistemon*, and *Eucalyptus*, while similar elements containing clustered crystals are found in species of *Myrtus*, *Eugenia*, and also in *Syzygium Jambolanum*. In conclusion, the abundance of tannin in the tissues of the cortex may be specially mentioned.

The **pith** is homogeneous in the cases more particularly investigated by Mentovich (species of *Myrtus*, *Melaleuca*, *Metrosideros*, and *Eucalyptus*).

B. Lecythidaceae

(Tribes Lecythideae, Barringtonieae, Napoleoneae.)

2 B. Structure of the Leaf[1]. The **mesophyll** usually has bifacial structure. Centric leaf-structure, however, also occurs, e. g. in *Foetidia mauritiana*, Lam. and *Asteranthos brasiliensis*, Desf. The **stomata** for the most part occur only on the lower side of the leaf (exceptions: *Lecythis lanceolata*, Poir., *Gustavia augusta*, L., *Foetidia mauritiana*, in which a few, and *Barringtonia acutangula*, Roxb., in which many stomata are also met with on the upper side), and are as a rule wedged in between three epidermal cells. Exceptionally (in *Chytroma Idatimon*, Miers) subsidiary cells arranged parallel to the pore occur. The leaf of *Napoleona Whitfieldii*, Decne., in addition to the ordinary stomata, shows others which are distinguished by their specially large size, and are to be found even on the young leaves. In *Foetidia mauritiana* and *Barringtonia racemosa*, Roxb., a one-layered hypoderm occurs beneath the epidermis on the upper side of the leaf. According to Lignier, horizontal division-walls are found in the **epidermal cells** on the upper side of the leaf in

[1] The following description of the structure of leaf and axis is essentially based on Lignier's work, Rech. sur l'anatomie des Lécythidées etc. His work is founded on the investigation of species of the genera *Gustavia*, *Berthalletia*, *Lecythis*, and *Couratari* in the tribe Lecythideae, of the genera *Barringtonia* and *Foetidia* in the tribe Barringtonieae and of both the genera of the tribe Napoleoneae, viz. *Napoleona* and *Asteranthos*. In this enumeration the genera are taken as delimited in Durand's Index.

Eschweilera parviflora, Miers (confounded with gelatinization ?). Papillose differentiation of the lower epidermis has been observed in *Lecythis racemiflora*, Sagot and *Couratari guianensis*, Aubl. The parenchymatous tissues of the leaf and, we may add, those of the axis also, are characterized by tannin-contents. In the axis the tannin is found in special cells, which form filamentous rows. The secretory cavities, which are characteristic of the Myrtaceae sens. str., are completely absent in the Lecythidaceae. An anatomical feature of a more special kind, observed only in *Asteranthos*, is the occurrence of sclerenchymatous fibres running irregularly in the mesophyll. As regards the mode of excretion of **oxalate of lime**, the Napoleoneae possess solitary crystals, the Lecythideae solitary and clustered prismatic crystals, the Barringtonieae star-like clustered crystals. In the leaf the crystals occasionally occur in the epidermis (*Chytroma Idatimon*, Miers). The **hairy covering**, like that of the rest of the Myrtaceae, is very simple. In the Napoleoneae hairs are absent; in the Lecythideae they are generally unicellular, short, stiff, and pointed, sometimes like papillae; in the Barringtonieae, finally, they are longer, uniseriate, and composed of 2 or 3 cells. Lignier has described and figured gland-like hairs in *Lecythopsis rufescens*, Berg, only; they are occasionally placed together in small groups, and appear as short, for the most part uniseriate hairs. Lastly, we may mention the paired, relatively large glands, which are borne on the base and lower side of the leaf in *Napoleona*. Their structure recalls the well-known glands on the leaf of the cherry-laurel; the secretory cells are narrow, thin-walled cells of palisade-like shape.

The appearance of the **petiole** in transverse section is characteristic of the individual tribes. In the Napoleoneae it shows only a single vascular arc of five bundles (Lignier's 'faisceaux principaux'), in the Lecythideae and Barringtonieae numerous vascular bundles, which are orientated in two or three concentrically arranged arcs (Lignier's 'faisceaux principaux, antérieurs, postérieurs'). In the structure of the petiole the Lecythideae, with the exclusion of the genus *Gustavia*, agree most closely with the Napoleoneae. In the Lecythideae the transverse section of the petiole shows an arc of principal vascular bundles ('faisc. principaux') and a bundle-system ('faisc. antérieurs'), which faces the upper side of the arc—the leaf being supposed to be in its natural position on the shoot. In *Gustavia* there are not only additional vascular bundles ('faisc. antérieurs') above the arc of principal bundles ('faisc. principaux'), but also others ('faisc. postérieurs') below them; in this case, as in the rest of the Lecythideae, all the vascular bundles are normally orientated, i. e. in the vascular bundles of the three or two arcs respectively the xylem lies on the upper, the bast on the lower side. The Barringtonieae, like *Gustavia*, also have three systems of vascular bundles; they differ from the Lecythideae, however, in the fact that the bundles of the lowest system ('faisc. postérieurs') are inversely orientated with regard to the position of wood and bast; that is to say, the bast is above and the xylem below.

3 B. Structure of the Axis. The complete absence of intraxylary soft bast in the Lecythidaceae, in contradistinction to what is found in the Myrtaceae sens. strict., may first be pointed out once more. On the other hand, **cortical vascular bundles** are present in the Lecythidaceae. Since they were first noticed by Guillard, they have been observed by different investigators (Dufour and Costantin, Solereder, Lignier) in the genera *Gustavia*, *Bertholletia*, *Lecythis*, *Couratari*, *Barringtonia*, *Foetidia*, *Careya*, *Planchonia*, *Napoleona*, and *Asteranthos*. In the Barringtonieae (*Barringtonia*, *Foetidia*, *Careya*, *Planchonia*) the cortical bundles are inversely orientated, the xylem lying outwards, the bast inwards; while the cortical bundles of the Lecythideae and Napoleoneae show the xylem normally situated on the inner, and the phloem on t

outer side. Owing to this diverse orientation of the xylem and phloem of the cortical bundles, one is thus easily enabled to distinguish a member of the Barringtonieae from the rest of the Lecythidaceae. The number of cortical bundles further affords a distinction between the two other tribes. In the Napoleoneae the number of the cortical bundles amounts to only four, in the Lecythideae to more than eight.

The course of the vascular system and the production of cortical bundles in the Lecythidaceae has been studied in detail by Lignier. The results of his investigations are of systematic value, and must therefore be shortly touched upon. As has been mentioned above, the petiole of the Napoleoneae possesses only a simple arc of five vascular bundles ; of these the middle three, fused into one bundle, pass into the normal bundle-ring of the axis ; the two laterally placed strands become normally orientated cortical bundles in the axis. In the Lecythideae the petiole possesses three or two systems of vascular bundles, either a principal system and an upper and lower system, or only a principal and an upper system (see above). Of the principal system the middle three vascular bundles pass into the bundle-ring of the axis ; the others become normally orientated cortical bundles in the axis ; the bundles situated below the principal system in the petiole and occurring only in *Gustavia*, form normally orientated cortical bundles in the axis ; the majority of the petiolar bundles situated below the principal system fuse with the principal bundle-system of the petiole, and only two become normally orientated cortical bundles in the axis. It has been stated above that the petiole of the Barringtonieae exhibits three bundle-systems, of which the lowest is inversely orientated as regards the position of wood and bast. Of the bundles of the middle system (the principal one), only the middle one passes into the bundle-ring of the axis ; the others in their further course turn through 180° and appear as inversely orientated cortical bundles in the axis. Of the bundles situated above the principal system the majority fuse with the latter, as in the Lecythideae ; two lateral ones turn in their course through 180° and form inversely orientated cortical bundles in the axis. Lastly, the lowest vascular bundles of the petiole, which are inversely orientated in the Barringtonieae, pass into the axis and there present themselves as inversely orientated cortical bundles.

The following points may be added with regard to the other structural features of the axis in the Lecythidaceae.

The **wood** consists of vessels with small or moderately wide lumina (diameter of vessel = ·02 mm. in *Foetidia mauritiana*, Lam., ·05 mm. in *Lecythis racemiflora*, Sag., ·1 mm. in *L. corrugata*, Poit.) and simple perforations, of simple-pitted wood-prosenchyma, usually abundantly developed wood-parenchyma and narrow medullary rays. The wood-parenchyma mostly forms tangential bands between the wood-fibres (*Lecythis ovalifolia*, DC., *Couratari Tauari*, Berg and others) ; in *Eschweilera subglandulosa*, Miers, and *Foetidia mauritiana*, Lam., it is developed in such abundance that it makes up the groundwork of the wood.

In the Lecythidaceae the **cork** arises superficially, either subepidermally, or at any rate a very little way below the epidermis. As a rule it is composed of flat cork-cells ; in *Gustavia augusta*, L., *Cariniana brasiliensis*, Casar. and *Lecythopsis rufescens*, Berg, the cork is stratified in a manner similar to that in the Myrtaceae sens. strict. The bast shows the same stratification into hard and soft bast as in the rest of the Myrtaceae.

Finally, mention may be made of the occurrence of gum-canals in the **pith** of some Lecythidaceae, namely in *Bertholletia excelsa*, Humb. et Bonpl., *Couratari guianensis*, Aubl., *Lecythis racemiflora*, Sag., and *Eschweilera parviflora*, Miers. According to Lignier these canals are ·2–·5 mm. wide, and are probably lysigenous.

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MELASTOMACEAE.

1. Review of the Anatomical Features. The Melastomaceae are at once excellently characterized by the external features of their vegetative organs, i. e. by the opposite, exstipulate, and mostly 3-9-veined leaves. Turning to anatomical characters, we may add the occurrence of intraxylary phloem, and the frequent appearance of medullary and cortical vascular bundles. The latter are also of importance for the diagnosis of tribes and genera. The wood consists of (1) vessels with simple perforations and with bordered or simple pitting in contact with ray-parenchyma; (2) of wood-parenchyma, which is usually little developed; and (3) of wood-prosenchyma, which either has simple pits, and in that case is commonly septate (in the Melastomeae hitherto investigated, as well as in *Astronia*) or bordered pits (Memecyleae, *Kibessia*). Interxylary phloem is characteristic of the genera *Kibessia, Memecylon, Mouriria* and *Pternandra*. The cork either arises in the pericycle or superficially, i.e. in the epidermis or in the first or second cell-layer of the primary cortex. The external limit of the pericycle is often formed by a distinct endodermis; the pericycle occasionally contains bast-fibres. The stomata are for the most part surrounded by several ordinary epidermal cells; subsidiary cells, placed parallel or transversely to the pore, are rare. The hairy covering consists of clothing and glandular hairs, and is extremely variable (see p. 361 and Fig. 79). Typical internal secretory organs are wanting; gelatinization of the epidermis of the leaf is very rare (*Marcetia acerosa*, DC.) in the Suborder Melastomeae, common in *Mouriria*. Oxalate of lime is usually excreted in the form of clustered crystals, more rarely in that of styloids (in *Astronia, Beccarianthus, Bellucia, Calycogonium, Centradenia, Henriettea, Henriettella, Kibessia, Loreya, Memecylon, Mouriria, Myriaspora*, and *Pternandra*), whilst ordinary rhombohedral solitary crystals are wanting.

In many cases the clustered crystals are replaced by sphaerites, in one case (*Aciotis*) by crystal-sand, composed of small needles. Of anatomical characters which may be utilized for special diagnosis, the following may be mentioned: small stomatal pits on the lower side of the leaf in species of *Mouriria* (Fig. 78); various features of the epidermis of the leaf, such as palisade-like elongation or papillose differentiation of the cells of the upper epidermis; development of hypoderm in the leaf; occurrence of sclerenchymatous fibres or spicular cells and (in *Aciotis annua*, Tr.) of spiral tracheides in the mesophyll; formation of aerenchyma in the stem.

2. STRUCTURE OF THE LEAF. The leaf-structure of this large Order is still far from being adequately investigated. The following statements extend to some few genera[1] investigated by Lignier, to the Memecyleae which formed the subject of certain researches by Van Tieghem, and to those genera of the tribes Microlicieae and Tibouchineae[2] examined by Pflaum.

The leaf-structure is either bifacial or centric. The **stomata** either occur on both sides of the leaf or only on the lower side. The mode of development, described by Lignier in the genera investigated by him (with the exception of *Memecylon*), and sometimes even to be recognized in the mature leaf, is certainly not universal; in this case the mother-cell of the guard-cells is cut out from an original epidermal cell by a single convex vertical wall. Usually the stomata of the mature leaf are surrounded by several ordinary epidermal cells. In other cases the pairs of guard-cells are wedged in between three neighbouring cells (*Rhynchanthera cordata*, DC.), or are accompanied by two subsidiary cells, arranged transversely (species of *Marcetia* and *Microlicia*) or parallel to the pore (*Memecylon clausiflorum*, according to Lignier). In certain species of *Microlicia* and *Pterolepis* the stomata lie with their pores parallel to one another, and to the median vein of the leaf. A very peculiar feature, characteristic of most species of the genus *Mouriria*, according to Van Tieghem, is the restriction of the stomata to small pits on the lower side of the leaf (Fig. 78). The pits vary in structure, and may have either a wide or a narrow opening. Occasionally the epidermal cells, situated between the stomata in the pits, are produced into short hairs or papillae (*Mouriria elliptica* and *M. Pusa*).

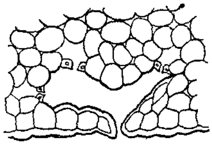

FIG. 78. Stomatal pit of *Mouriria eugeniaefolia*.—After Van Tieghem.

Regarding the structure of the **epidermis** of the leaf, the following facts may be mentioned. According to Pflaum the epidermis, and especially that on the upper side of the leaf, is in many cases characterized by the wide lumina of its cells, and by the gelatinous appearance of its cellulose membranes. Gelatinization of the epidermis of the leaf is certainly very rare in the Sub-order Melastomeae, and at the present time is only known in *Marcetia acerosa*, DC. In the genus *Mouriria*, on the other hand, it occurs frequently, to judge from Van Tieghem's statements, and from my own observation of it in *Mouriria parvifolia*, Benth.; Van Tieghem, however, described the muci-

[1] These are *Centradenia*, *Nepsera*, *Lasiandra*, *Monochaetum*, *Sonerila*, *Phyllagathis*, *Amphiblemma*, *Bertolonia*, *Medinilla*, *Miconia*, *Sphaerogyne*, and *Memecylon*.

[2] Namely: *Cambessedesia*, *Pyramia*, *Chaetostoma*, *Microlicia*, *Trembleya*, *Lavoisiera*, *Rhynchanthera*, *Siphanthera*, *Centradenia*, *Poteranthera*, *Acisanthera*, *Heeria*, *Arthrostemma*, *Nepsera*, *Desmoscelis*, *Microlepis*, *Brachyotum*, *Svitramia*, *Macairea*, *Schwackaea*, *Pterolepis*, *Tibouchina*, *Comolia*, *Fritzschia*, *Marcetia*, and *Aciotis*. Investigations on the leaf-structure of the other tribes are in progress.

laginous inner walls, which very frequently enclose cellulose-lamellae, as peculiarly thickened cell-walls, which is not correct. We may add that similar cells with mucilaginous membranes also occur abundantly in the parenchyma of the larger veins in *M. parvifolia*. According to Pflaum, the upper epidermis of the leaf in species of *Cambessedesia*, *Pyramia*, and *Marcetia* is characterized by palisade-like elongation. Papillose differentiation of the upper epidermis is described by Lignier in *Monochaetum umbellatum*, '*Bertolonia mirandra*,' *Sphaerogyne latifolia*, and *Miconia peruviana*, and by Pflaum in *Rhynchanthera cordata*, DC., *Marcetia bracteolaris*, Cogn., and *Aciotis indecora*, Triana. A locally two-layered epidermis is, according to Pflaum, found on the upper side of the leaf in species of *Comolia*; on the same side hypoderm of varying thickness occurs in a number of species, thus, according to Van Tieghem in *Astronia glabra*, *A. macrophylla*, *A. spectabilis*, *Mouriria acutiflora*, and *M. spathulata*, according to Johow in certain West Indian epiphytic species of *Blakea* (not more precisely named), according to Lignier and Krasser in *Medinilla Curtisii*, *M. farinosa*, *M. javanensis*, Bl., *M. magnifica* and *M. speciosa*, and according to Pflaum in *Marcetia ericoides*, Cogn., *M. tetrasticha*, Cogn., as well as in species of *Microlepis*, *Tibouchina*, and *Macairea* (in the last-named genus the hypoderm is sometimes strongly developed above the vascular bundles of the veins, and projects into the mesophyll in the form of a ridge).

According to a verbal communication from Herr Palézieux, the mesophyll of *Pachyloma coriaceum*, DC. has quite a peculiar structure; in this plant the cell-walls of the spongy tissue are provided with the same local thickenings as in certain Menispermaceae (see p. 40).

In the veins, mechanical tissue accompanying the vascular bundle is rarely developed, and when present either directly adjoins the vascular bundle or is separated from it and situated subepidermally (the latter condition occurring in species of *Chaetostoma*, *Microlicia*, *Lavoisiera*, and *Microlepis*). More commonly there are sclerenchymatous cells, resembling rod-cells, in the parenchyma of the ground-tissue in the larger veins. In this connexion the following structural features remain to be mentioned: according to Pflaum the variously shaped sclerenchymatous cells with a large lumen in the mesophyll of species of *Lavoisiera* and *Microlicia*; the spiral tracheides traversing the mesophyll in *Aciotis annua*, Triana, and the sclerenchymatous fibres present in the same tissue in *Macairea Spruceana*, Berg; according to Van Tieghem, the occurrence of sclerenchyma-fibres or spicular cells in the mesophyll in the species of the genera *Memecylon* and *Mouriria* and in the monotypic genus *Plethiandra*. The varied form of the sclerenchymatous cells in the mesophyll is of great value for the diagnosis of the species of *Memecylon* and *Mouriria*.

Van Tieghem distinguishes four types of the elements in question in the genus *Memecylon*, of which he investigated sixty-six species: I. Sclerenchyma-fibres, running irregularly through the entire mesophyll, penetrating as far as the upper and lower epidermis, and spreading out beneath each as a regular layer; these sclerenchyma-fibres are (*a*) unlignified in *Memecylon angustifolium*, *M. capitellatum*, *M. cordatum*, *M. Elaeagni*, *M. ellipticum*, *M. floribundum*, *M. grandifolium*, *M. myrtiforme*, *M. oleaefolium*, *M. strumosum*, *M. sylvaticum*, *M. ulopterum*; (*b*) more or less strongly lignified in *M. amplexicaule*, *M. angulatum*, *M. caeruleum*, *M. edule*, *M. excelsum*, *M. ferreum*, *M. Hookeri*, *M. ligustrinum*, *M. myricoides*, *M. orbiculare*, *M. ovatum*, *M. ovoideum*, *M. Preslianum*, *M. prunifolium*, *M. rhamnoideum*, *M. rhinophyllum*, *M. sphaerocarpum*, *M. tinctorium*, *M. umbellatum*. In a series of species, which also belong to this type, the sclerenchyma-fibres run more in the middle plane of the leaf, and bend out obliquely towards the epidermis, continuing their course beneath the latter; these are *M. australe*, *M. costatum*, *M. depressum*, *M. dolichophyllum*, *M. dumosum*, *M. garcinioides*, *M. Griffithianum*, *M. heteropleuron*, *M. laurinum*, *M. myrsinoides*, *M. paniculatum*, *M. parvifolium*, *M. pauciflorum*, *M. prasinum*, *M. revolutum*, *M. rostratum*, *M. tenuicaule*, *M. Thomsoni*. II. Branched scleren-

chymatous cells (spicular cells) occur, whilst fibres are wanting in *M. Arnottianum*, *M. fasciculare*, *M. Gardneri*, *M. lutescens*, *M. melastomoides*, *M. oligoneuron*, *M. phyllanthifolium*, *M. Spathandra*, *M. trinerve*, *M. varians*, *M. Vogelii*. III. The following possess forms intermediate between I and II, namely branched and elongated sclerenchymatous cells, which traverse the mesophyll almost perpendicularly and terminate in the form of a T beneath the epidermis: *M. cuneatum*, *M. leucanthum*, *M. macrophyllum*. IV. Forms intermediate between I and II, namely, elongated columnar sclerenchyma-fibres, traversing the leaf perpendicularly and having a few small branches, are found in *M. Heyneanum* and *M. scutellatum*.

In the genus *Mouriria* Van Tieghem distinguishes three forms: I. very long sclerenchyma-fibres, running irregularly in the entire mesophyll and finally forming a layer beneath each epidermis in *Mouriria Apiranga*, *M. crassifolia*, and *M. eugeniaefolia*; II. long branched sclerenchyma-fibres, traversing the leaf-tissue approximately at right angles in *M. abnormis*, *M. arborea*, *M. Gardneri*, and *M. Pusa*; III. star-shaped spicular cells, situated in the middle of the mesophyll in *M. acutiflora*, *M. angustifolia*, *M. brevipes*, *M. cauliflora*, *M. elliptica*, *M. emarginata*, *M. excoriata*, *M. guianensis*, *M. lanceolata*, *M. parvifolia*, *M. pauciflora*, *M. princeps*, *M. Sagotiana*, *M. Sideroxylon*, *M. spathulata*, *M. Valenzuelana*, and *M. vernicosa*.

The sclerenchymatous elements in the leaf of *Plethiandra Mottleyi* are branched spicular cells.

Special secretory receptacles do not occur in the Order. **Oxalate of lime** is usually found in the form of clustered crystals, those occurring in the mesophyll being occasionally distinguished by their considerable size, and in that case giving rise to transparent dots in the leaf Ordinary large rhombohedral solitary crystals have not been met with in any member of the Order. In the neighbourhood of the bases of the shaggy hairs ('Zottenfüsse'), to be discussed later, the clustered crystals are often replaced by sphaerites. In *Aciotis longifolia*, Tr., the clustered crystals are loosely built up of small crystalline needles, while in *Aciotis annua*, Tr., crystal-sand, consisting of small acicular crystals, appears in their place. Lastly, styloids have been observed in the genera *Mouriria* and *Memecylon* of the Memecyleae, in the genera *Astronia*, *Beccarianthus*, *Kibessia*, and *Pternandra* of the Astronieae, in the genera *Bellucia*, *Calycogonium*, *Henriettea*, *Henriettella*, *Loreya*, and *Myriaspora* of the Miconieae, as well as (according to Lignier and Pflaum) in *Centradenia* pro parte (*C. inaequilatera*, Don). In a certain number of these genera clustered crystals are present in addition to the styloids, e.g. in species of *Memecylon* and of *Mouriria*, in which the styloids occur in the axis, and the clustered crystals in the leaf; in *Centradenia floribunda*, Planch., clustered crystals occur in the leaf-tissue (Fig. 79, *A*), some of their individual crystals being differentiated like styloids.

The **hairy covering** is very variable. The following types of clothing hairs are found: unicellular trichomes differentiated like papillae (*Marcetia*, *Macairea*); uni- or bi-seriate trichomes with thick walls and I-shaped lumina; very rarely (*Trembleya laniflora*, Cogn.) long uniseriate trichomes; very frequently shaggy hairs of conical or filiform shape or showing considerable surface expansion; brush-like shaggy hairs, i.e. hairs with a multiseriate filiform stalk and terminal cells arranged like the hairs of a paint-brush (*Sphaerogyne latifolia*, Fig. 79, *B*); shaggy hairs of the candelabra type with a parenchymatous stalk occasionally crowned by a glandular head on a long pedicel (*Pyramia*, Fig. 79, *C*); candelabra-hairs (*Medinilla farinosa*, Fig. 79, *D*); stellate hairs with a short stalk and unicellular rays (*Miconia Pavoniana*); and lastly, peltate hairs (according to O. Bachmann in *Astronia papetaria*, Bl., where they have the same structure as in the Combretaceous genus *Thiloa*). Of these forms the shaggy hairs, which are usually filiform, have a varied and often really remarkable structure. According as they are composed of parenchyma or of prosenchyma or of both, they may be distinguished as parenchymatous or prosenchymatous shaggy hairs, or as parenchymatous hairs in the interior

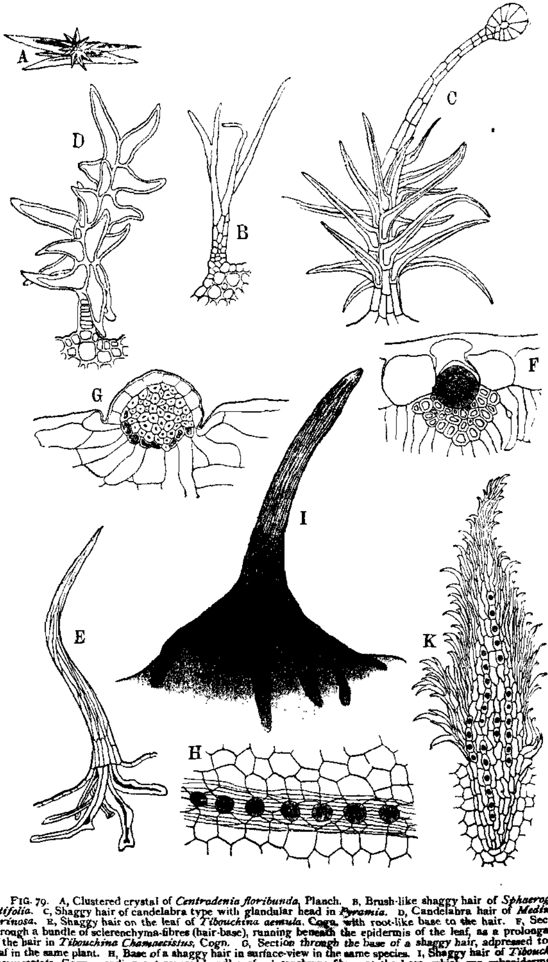

FIG. 79. A, Clustered crystal of *Centradenia floribunda*, Planch. B, Brush-like shaggy hair of *Sphaerogyne latifolia*. C, Shaggy hair of candelabra type with glandular head in *Pyramia*. D, Candelabra hair of *Medinilla farinosa*. E, Shaggy hair on the leaf of *Tibouchina aemula*, Cogn., with root-like base to the hair. F, Section through a bundle of sclerenchyma-fibres (hair-base), running beneath the epidermis of the leaf, as a prolongation of the hair in *Tibouchina Chamaecistus*, Cogn. G, Section through the base of a shaggy hair, adpressed to the leaf in the same plant. H, Base of a shaggy hair in surface-view in the same species. I, Shaggy hair of *Tibouchina decemcostata*, Cogn., sending out several bundles of sclerenchyma-fibres at the base, which run subepidermally. K, Scale-like shaggy hair of *Tibouchina Mathaei*, Cogn.—A, C and K after Pflaum, B and D after Lignier: the remainder original.

of which a bundle of sclerenchyma-fibres runs. Additional sclerenchyma is in many cases connected with the body of the hair in the prosenchymatous shaggy hairs, or with the bundle of sclerenchyma in the parenchymatous hairs; this sclerenchyma penetrates into the interior of the organ, in this manner firmly anchoring the shaggy hair and determining a certain position of the latter with regard to the surface of the organ. The sclerenchyma ('base of shaggy hair') either consists of a bundle of fibres which branches like a root (Fig. 79, *E*), or of a strand which travels for a variable distance beneath the epidermis of the leaf, either remaining simple (Fig. 79, *F–H*) or dividing into several strands (Fig. 79, *I*); in both cases it is accompanied by crystal-cells with clustered crystals or sphaerites. Other variations concern the body of the prosenchymatous shaggy hairs, for the tips of the superficial cells are frequently differentiated in a papillose manner (species of *Heeria, Desmoscelis, Brachyoton, Pterolepis,* and *Tibouchina*), or a more fundamental separation of the superficial cells is found, leading to a differentiation like that of hairs of the fir-tree or candelabra type (species of *Microlepis, Brachyoton,* and *Tibouchina*). The shaggy hairs which are differentiated like scales (Fig. 79, *K*), and have already been shortly referred to above, resemble a moss-leaf in shape, and have been observed in *Pterolepis striphnocalyx,* Cogn., *Tibouchina Mathaei,* Cogn., and *T. verticillaris,* Cogn. The external glands observed in the Order may be divided into three categories: firstly, small multicellular external glands, which are either club-shaped or have a variously shaped multicellular head sharply delimited (very common, see Lignier and Pflaum); secondly, bladder-like integumental glands, having the structure of the glands of the Labiatae (according to Pflaum in *Chaetostoma, Microlicia, Trembleya, Lavoisiera,* and *Macairea*; occasionally we find transitions to similarly constructed external glands without noticeable elevation of the cuticle, as in *Microlicia, Siphanthera,* and *Fritzschia*); thirdly and lastly, glandular shaggy hairs, that is to say, shaggy hairs with the varied structure already referred to, which are surmounted by a multicellular glandular head. In connexion with the external glands, the occurrence of cork-warts on the lower side of the leaf of *Pachyloma coriaceum,* DC., may be briefly mentioned (according to a verbal communication from Herr Palézieux).

According to Lignier, the uniform feature in the structure of the **petiole** lies in the fact that the principal system of fibro-vascular tissue is arc-shaped, and consists of isolated vascular bundles. On the other hand, numerous modifications are found with regard to the occurrence of accessory bundles, and their varied arrangement, details regarding which may be obtained by reference to the works of Plitt and Lignier.

3. Structure of the Axis. As already stated in the general review, the Melastomaceae are characterized by the possession of **intraxylary phloem.** A considerable number of genera and species [1] have been investigated with regard to the structure of their axis by different authors (Vöchting, Solereder, Lignier, and recently by Van Tieghem especially), and intraxylary phloem has been demonstrated in all cases. In very many (but not in all) species, **medullary** and **cortical vascular bundles** are present in addition to the intraxylary phloëm; these bundles are mostly concentric in structure, and in that case are provided with centrally placed xylem. Moreover, in the same species we find either cortical bundles only, or medullary bundles only, or both medullary and cortical bundles at the same time; in a small portion of the species the vascular bundles are absent in both pith and cortex. The medullary bundles may appear in varied numbers, either few or

[1] See the enumeration of genera and species on p. 359 et seq. and p. 364 et seq.

many; in some cases only a single vascular bundle occurs at the centre of the pith. The species with cortical bundles are, as a rule, at once distinguishable externally by their four-angled branches; the cortical bundles generally occur singly or several together in the angles of the branch; in rarer cases they are also found in the cortical parenchyma between the angles. Both in the medullary and in the cortical fibro-vascular strands, the xylem is occasionally so much reduced as to disappear entirely. According to the statements of J. E. Weiss and Lignier, the medullary bundles are in genetic connexion with the intraxylary soft bast. That is, they are nothing more than the direct continuation of the phloem-bundles, running in the marginal part of the pith in a higher internode; these on passing into the node penetrate into the more central part of the pith, being at the same time often accompanied by the primary vessels of the bundle-ring—the spiral and annular tracheae. The cortical bundles either represent the lateral strands of the leaf-trace, running in the angles of the stem, or they are branches of these strands; more rarely the median strand of a leaf-trace furnishes a cortical bundle. Finally, the girdle-like strands connecting the cortical bundles at the node also deserve notice.

In the subsequent tables, indicating the occurrence of medullary and cortical vascular bundles in the Melastomaceae and based on the observations accumulated up to the present time, the following abbreviations are made use of: C, M, = cortical and medullary bundles; Cp, Mp = cortical or medullary bundles respectively, consisting of phloem only; f, s, m, 4, 1, or some other number, placed before the C or M, signifies the number of cortical or medullary bundles respectively; f = few, s = several, m = many. The abbreviations in question are appended to the name of the species or genus or tribe, of which that feature of the cortical or medullary bundles expressed by them is characteristic; where abbreviations are omitted, detailed statements as to the features in question do not exist.

I. Medullary bundles alone occur in: Tribe 1. Microlicieae: *Lithobium cordatum*, s, Mp; *Eriocnema acaulis*, *E. fulva*, f, M.—Tribe 3. Osbeckieae: *Dinophora spenneroides*, f, Mp; *Nerophila gentianoides*, f, Mp.—Tribe 5. Merianieae, f–m, M: *Huberia laurina*, *H. ovalifolia*; *Benevidesia organensis*; *Behuria insignis*; *Adelobotrys scandens*; *Meriania grandidens*, *M. leucantha*, *M. purpurea*, *M. speciosa*, *M. splendens*; *Graffenrieda conostegioides*, *G. Moritziana*; *Axinaea affinis*, *A. lepidota*, *A. scutigera*; *Calyptrella Galeottii*, *C. tristis*; *Centronia brachycera*, *C. excelsa*.—Tribe 6. Oxysporeae: *Oxyspora paniculata*, f–s, M, *O. vagans*; *Bredia Oldhami*, 1 M; *Driessenia axantha*, 1 M; *Blastus parviflorus*, f–s, M; *Allomorphia exigua*; *Ochthocharis bornensis*, *O. javanica*; *Veprecella schizocarpa*, 5 M; *Rousseauxia chrysophylla*, f–s, M; *Kendrickia Walkeri*; *Phornothamnus thymoides*, 1 M.—Tribe 7. Sonerileae: *Phyllagathis rotundifolia*; *Calvoa sinuata*; *Amphiblemma cymosum*; *Brittenia subacaulis*, 1 M; *Gravesia guttata*.—Tribe 8. Bertolonieae: *Bertolonia marmorata*, *B. miranda*, *B. pubescens*, 1 M; *Macrocentrum cristatum*, Mp; *Salpinga longifolia*, f, M; *Diplarpea paleacea*, m, M; *Monolena ovata*, *M. primulaeflora*, s, M; *Diolena auriculata*, f, M; *Triolena scorpioides*, 1 M.—Tribe 9. Dissochaeteae: *Sakersia africana*, m, M; *Dalenia pulchra*, m, M; *Marumia nemorosa*, m, M; *Dissochaeta superba*, m, M; *Anplectrum*, m, M, *cyanocarpum*, *A. pallens*, *A. rostratum*; *Creochiton pudibunda*, m, M; *Omphalopus fallax*, m, M; *Carionia elegans*, s, M; *Medinilla Curtisii*, *M. farinosa*, f, M, *M. magnifica*, *M. rubicunda*, *M. Sieboldiana*, *M. speciosa*; *Medinillopsis Beccariana*, *M. sessiliflora*; *Pachycentria constricta*, *P. tuberculata*; *Pogonanthera pulverulenta*; *Boerlagea grandifolia*.—Tribe 10. Miconieae: *Platycentrum clidemioides*; *Leandra quinquedentata* (*Oxymeris quinquedentata*), *L. rufescens* var. (*Oxymeris asperiuscula*), *L. scabra*; *Calycogonium heterophyllum*, *C. rhamnoideum*, *C. stellatum*; *Pachyanthus cubensis*, *P. oleaefolius*; *Pterocladon Sprucei*; *Anaectocalyx bracteosa*; *Conostegia clidemioides*, *C. speciosa*; *Charianthus coccineus*, *C. glaberrimus*; *Tetrazygia albicans*, *T. elaeagnoides*, 4 M, *T. villosa*; *Miconia calvescens*, *M. chrysoneura*, m, M, *M. desmantha*, *M. metallica*, *M. magnifica*; m, M, *M. Pavoniana*; *Pleiochiton ebracteatum*, s, Mp; *Catocoryne linnaeoides*, s, Mp; *Heterotrichum macrodon*, *H. patens*; *Tococa formicaria*, *T. latifolia*, *T. spadiciflora*; *Microphysca quadrialata*; *Maieta guianensis*, *M. Poeppigii*, *M. testiculata* (*Calophysa testiculata*); *Myrmidone macrosperma*, 3 M; *Clidemia blepharodes*, *C. guadalupensis*

(*Sagraea guadalupensis*), *C. hirta*, *C. impetiolaris* (*Calophysa pilosa*), *C. obliqua* (*Sagraea obliqua*), *C. plumosa* (*Sagraea plumosa*); *Mecranium haemanthum*; *Bellucia circumscissa*, *B. grossularioides*; *Ossaea acuminata*, *O. angustifolia*, *O. bracteata*, *O. leptopus*, *O. Lima*, *O. scabrosa*, *O. scalpta* (*Sagraea scalpta*).—Tribe 11. Blakeae: *Blakea*, m, M, *anisophylla*, *B. laurifolia*, *B. pulverulenta*, *B. pyxidanthus*, *B. repens*, *B. rosea*, *B. trinervia*; *Topobea*, m, M, *calycularis*, *T. glaberrima*, *T. longipes*, *T. parasitica*, *T. stephanochaeta*.—Tribe 12. Astronieae: *Astronia*, m, M, *fraterna*, *A. glabra*, *A. macrophylla*, *A. papetaria*, *A. pileolata*, *A. spectabilis*; *Beccarianthus pulcher*, m, M; *Plethiandra Motleyi*, 1 Mp.

II. Cortical bundles alone occur in: Tribe 1. Microlicieae, 4 C: *Castratella piloselloides*; *Cambessedesia Espora*, *C. latevenosa*; *Pyramia pityrophylla*, *P. salviaefolia*, *P. striatella*; *Stenodon gracilis*, *S. suberosus*; *Chaetostoma castratum*; *Microlicia cordata*, *M. hirsutissima*, *M. variolosa*, *M. vestita*; *Trembleya pityoides*; *Lavoisiera alba*, *L. caryophyllea*, *L. firmula*, *L. grandiflora*, *L. microphylla*, *L. nervulosa*, *L. pulchella*, *L. pulcherrima*; *Rhynchanthera novemnervia*, *R. parviflora*, *R. pratensis*, *R. secundiflora*, *R. Weddellii*; *Siphanthera microlicioides*, *S. paludosa*; *Poteranthera crassipes*, *P. pauciflora*; *Tulasnea foliosa*.—Tribe 2. Tibouchineae, 4 C: *Marcetia canescens*, *M. latifolia*, *M. taxifolia*, *M. tenuifolia*, *M. tetrasticha*.—Tribe 13. Memecyleae: *Axinandra alata*, *A. Beccariana*, *A. coriacea*, *A. zeylanica*.

III. Medullary and cortical bundles are present in: Tribe 1. Microlicieae: *Bucquetia glutinosa*, 1 Mp + 4 C; *Centradenia floribunda*, *C. rosea*, 1 M, or 1 Mp + 4 C.—Tribe 2. Tibouchineae: *Acisanthera hedyotidea*, *A. punctatissima*, *A. quadrata*, *A. recurva*; *Heeria rosea*, *H. subtriplinervia*, *H. undulata*, m, M; *Arthrostemma campanulare*, *A. Galeottianum*, *A. glomeratum*, s, C, *A. herbaceum*, s, C, *A. ladanoides*, *A. lutescens*, f, M, *A. Martiusianum*, 1 M; *Ernestia tenella*; *Appendicularia thymifolia*; *Nepsera aquatica*, 1 M; *Desmoscelis villosa*, f, M; *Microlepis oleaefolia*, m, M; *Brachyotum Benthamianum*; *Svitramia pulchra*; *Macairea* m, M, *adenostemon*, *M. stylosa*; *Pterogastra divaricata*, f, M; *Schwackaea cupheoides*; *Pterolepis versicolor*; *Tibouchina*, m, M, *Candolleana*, *T. Fontanesii*, *T. heteromalla*, s, C, *T. macrantha*, *T. petiolaris*; *Purpurella albiflora*, m, Mp; *Chaetolepis alpina*, *C. cubensis*, *C. Lindeniana*, *C. microphylla*, *C. satureioides*, 1 M; *Comolia Martiana*, f, Mp, *C. ovalifolia*, *C. Sertularia*, *C. stenodon*, *C. viscidula*; *Aciotis acutiflora*; in all 4 C is the rule.—Tribe 3. Osbeckieae: *Osbeckia chinensis*, 4 C, *O. nepalensis*, s, C + m, M; *Guyonia tenella*, 4 C; *Otanthera*, 4 C, *crinita*, f, M, *O. cyanoides*; *Tristemma hirtum*, m, M; *Antherotoma Naudinii*, 4 C; *Dissotis debilis*, 1–2 M; *Melastoma*, 4 C, *malabathricum*, *M. normale*, *M. repens*; *Dichaetanthera asperrima*, m, M, *D. latifolia*, m, M + s, C, *D. madagascariensis*, f, M, *D. rosea*, m, M; *Dionychia Bojerii*, 4 C + m, M; *Rhodosepala erecta*, f, Mp; *Barbeyastrum corymbosum*, s, Mp.—Tribe 4. Rhexieae: *Rhexia*, s, C + f–1 Mp, *mariana*, *R. virginica*; *Monochaetum*, 4 C, *Bonplandi*, 1–s, M or Mp, *M. meridense*, 1 Mp, *M. umbellatum*.—Tribe 5. Merianieae: *Acanthella Sprucei*, 4 C + s, M or s, Mp.—Tribe 6. Oxysporeae: *Amphorocalyx multiflorus*, s, C + s, M.—Tribe 9. Dissochaeteae: *Dicellandra Barteri*, 4 C + f, M.

IV. Lastly, medullary and cortical bundles are wanting in the following species: Tribe 2. Tibouchineae: *Fritzschia anisostemon*, *F. caespitosa*, *F. erecta*, *F. integrifolia*.—Tribe 5. Rhexieae: *Opisthocentra clidemioides*.—Tribe 6. Oxysporeae: *Barthea chinensis*; *Anerincleistus hirsutus*.—Tribe 7. Sonerileae: *Sonerila begoniaefolia*, *S. elegans*, *S. margaritacea*, *S. paradoxa*, *S. picta*, *S. robusta*, *S. solanoides*, *S. tomentella*; *Phyllagathis rotundifolia* (only in thin branches); *Sarcopyramis lanceolata*; *Gravesia angustifolia*, *G. bertolonoides*, *G. Humblotii*, *G. pedunculata*, *G. primuloides*, *G. reticulata*; *Calvoa sinuata* (in thin branches); *Amphiblemma cymosum* (in thin branches); *Bisglaziovia behurioides*.—Tribe 10, Merianieae: *Loreya acutifolia*, *L. ovata*, *L. Spruceana*; *Henriettea maroniensis*, *H. Martii*, *H. Patrisiana*; *Henriettella lateriflora*, *H. parviflora*, *H. trachyphylla*; *Ossaea microphylla*; *Myriaspora decipiens*, *M. egensis*.—Tribe 12. Astronieae: *Pternandra capitellata*, *P. cyanea*, *P. latifolia*; *Kibessia acuminata*, *K. azurea*, *K. cordata*, *K. cupularis*, *K. fuliginosa*, *K. galeata* (*Rectomitra galeata*), *K. Korthalsiana* (*Rectomitra cordata*), *K. simplex*, *K. subulata*, *K. tuberculata* (*Rectomitra tuberculata*).—Tribe 13. Memecyleae: *Mouriria abnormis*, *M. acutiflora*, *M. angustifolia*, *M. Apiranga*, *M. arborea*, *M. brevipes*, *M. cauliflora*, *M. crassifolia*, *M. elliptica*, *M. emarginata*, *M. Gardneri*, *M. guianensis*, *M. lanceolata*, *M. parvifolia*, *M. pauciflora*, *M. princeps*, *M. Pusa*, *M. Sagotiana*, *M. Sideroxylon*, *M. spathulata*, *M. Valenzuelana*, *M. vernicosa*; *Memecylon acuminatum*, *M. amplexicaule*, *M. angulatum*,

M. angustifolium, M. Arnottianum, M. australe, M. caeruleum, M. capitellatum, M. clausiflorum, M. cordatum, M. costatum, M. Cumingianum, M. cuneatum, M. depressum, M. dolichophyllum, M. dumosum, M. edule, M. Elaeagni, M. ellipticum, M. excelsum, M. fasciculare, M. ferreum, M. fuscescens, M. garcinioides, M. Gardneri, M. grande var. *Khasiana, M. Griffithianum, M. heteropleuron, M. Heyneanum, M. Hookeri, M. intermedium, M. laevigatum, M. laurinum, M. leucanthum, M. lilacinum, M. lutescens, M. melastomoides, M. myricoides, M. myrsinoides, M. oleaefolium, M. oligoneuron, M. orbiculare, M. paniculatum, M. parvifolium, M. pauciflorum, M. phyllanthifolium, M. polyanthemos, M. prasinum, M. Preslianum, M. revolutum, M. rhinophyllum, M. rostratum, M. scutellatum, M. Spathandra, M. sphaerocarpum, M. strumosum, M. sylvaticum, M. Thomsoni, M. tinctorium, M. trinerve, M. ulopterum, M. varians, M. Vitiense, M. Vogelii.*

If the above statements are examined, it will be found that, according to the investigations hitherto made, the occurrence of medullary or of cortical bundles only, as well as the simultaneous absence or occurrence of medullary and cortical bundles is, as a rule, important for generic diagnosis, or even for the diagnosis of the tribes, inasmuch as one of the anatomical features in question predominates in certain tribes. Medullary bundles alone, although not without exception, are characteristic of the tribes Merianieae, Oxysporeae, Bertolonieae (here without a known exception), Dissochaeteae, Miconieae, Blakeae (here without a known exception) and of those Astronieae which possess no interxylary phloem. In the same way the exclusive occurrence of cortical bundles distinguishes the tribe Microlicieae. The simultaneous occurrence of medullary and cortical bundles may be taken as a characteristic of the Tibouchineae, Osbeckieae, and Rhexieae. The absence of both is chiefly confined to the Sonerileae, a portion of the Miconieae, and to those Astronieae and Memecyleae which possess interxylary phloem.

In connexion with the detailed discussion of the medullary and cortical bundles, the occurrence of **interxylary phloem** in certain Melastomaceous genera belonging to the tribes Astronieae and Memecyleae, may be mentioned. It was first observed by me in *Memecylon, Mouriria,* and *Kibessia*, and recently by Van Tieghem also in *Pternandra*. From the systematic point of view it should perhaps be pointed out that *Astronia, Beccarianthus, Plethiandra,* and *Axinandra* have wood with normal structure, so that interxylary phloem does not represent a tribal peculiarity of the Astronieae and Memecyleae. On the other hand, the occurrence of interxylary phloem appears to be constant in the four genera named, for it has been demonstrated in all the species of the genera in question quoted above in the discussion of the medullary and cortical bundles. According to the researches of Lignier and Van Tieghem, the interxylary groups of soft bast in *Memecylon, Mouriria, Kibessia,* and *Ptermandra* originate in just the same manner as in *Strychnos*. The groups of soft bast are given off externally by the cambium; the activity of the strips of cambium situated between the external groups of soft bast and the wood ceases, and becomes replaced by cambial tissue, which arises on the outer side of the groups of soft bast, and again completes the cambium-ring.

No other anomalies occur in the structure of the stem in this Order, besides those already referred to, viz. bicollateral structure of the vascular bundles, medullary and cortical bundles, interxylary phloem.

Regarding the structure of the **wood**, the following statements are based on my earlier preliminary investigations [1]. The medullary rays in a transverse section of the wood are never broad, but only uni- or bi-seriate, and the vessels do not generally have wide lumina (maximum diameter = ·04–·07 mm.); it is only in the climbing species, e.g. in *Dyssochaete sagittata*, that the diameter of the

[1] The following plants were investigated: species of the genera *Rhynchanthera, Osbeckia, Rhexia, Meriania, Oxyspora, Sonerila, Medinilla, Ossaea,* and *Blakea*, among the Melastomeae, *Astronia* and *Kibessia* among the Astronieae, and *Mouriria* and *Memecylon* among the Memecyleae.

vessels attains ·3 mm., according to Schenck's statement. The nature of the pitting on the walls of the vessels, where they are in contact with parenchyma, varies. In the Melastomeae, simple pits commonly occur on these parts of the wall, e.g. in *Medinilla* and *Rhynchanthera*, or one finds bordered pits, which pass over into simple pits ; in the Memecyleae, bordered pitting is present at these points; in the Astronieae investigated, simple pitting. The bordered pits of the vessels sometimes possess the sieve pit-like structure discovered by Jönsson (species of *Astronia, Blakea, Medinilla, Meriania, Osbeckia, Ossaea, Oxyspora, Rhexia, Rhynchanthera, Sonerila*). The perforations of the vessels are always simple. The wood-parenchyma occurs in the neighbourhood of the vessels and is usually not conspicuously developed ; sometimes, e.g. in *Mouriria*, it occurs in greater abundance and is also present among the prosenchymatous elements. The pitting of the wood-prosenchyma varies. Further research is required to determine whether this character is of value for the diagnosis of the tribes or of the genera only. In the Melastomeae which I investigated, the wood-prosenchyma always bears simple pits ; occasionally (*Sonerila elegans*), however, the pits have quite a narrow border. This prosenchyma with simple pits frequently proved to be septate, by means of delicate cross-walls, in almost all members of the Melastomeae investigated (except *Rhexia virginica*, L.). The Memecyleae cited below have wood-prosenchyma bearing bordered pits, though the latter are not abundant. Among the Astronieae, *Astronia* agrees with the Melastomeae in having wood-prosenchyma with simple pits and occasional septa, whilst *Kibessia* agrees with the Memecyleae in possessing prosenchyma with bordered pits.

Van Tieghem's investigations furnish information regarding the structure of the **cortex**. In a certain number of the genera the cork arises superficially, in others deeply in the interior of the cortical tissue—in the 'pericycle.'

In the first case, where superficial cork-formation takes place, the outermost cell-layer of the primary cortex as a rule becomes the phellogen : e.g. in *Adelobotrys* of the tribe Merianieae ; in *Blastus, Bredia, Kendrickia,* and *Oxyspora* of the tribe Oxysporeae ; in *Calvoa* of the tribe Sonerileae ; in *Bertolonia* and *Salpinga* of the tribe Bertolonieae ; in *Boerlagea, Carionia, Dalenia, Medinilla,* and *Pachycentria* of the tribe Dissochaeteae ; in most of the Miconieae, namely, in *Calycogonium, Charianthus, Clidemia, Conostegia, Heterotrichum, Mecranium, Miconia, Microphysca, Ossaea, Pachyanthus, Platycentrum,* and *Tetrazygia,* also in *Henriettea, Henriettella, Loreya,* and *Myriaspora* ; in the genera *Blakea* and *Topobea* of the Blakeae ; lastly, in *Plethiandra* and *Beccarianthus* among the Astronieae. In *Astronia* (Astronieae) the cork-cambium originates in the second cell-layer of the cortex, in *Diplarpea* (tribe Bertolonieae), *Amphiblemma* (tribe Sonerileae) and *Medinillopsis* (tribe Dissochaeteae) in the epidermis. On the other hand, a more or less deeply seated cell-layer of the pericycle becomes the cork-cambium in the Microlicieae, in the Tibouchineae and Osbeckieae, in *Benevidesia, Calyptrella, Centronia,* and *Meriania* of the tribe Merianieae, in *Amphorocalyx, Anerincleistus,* and *Ochthocharis* of the tribe Oxysporeae, in *Sakersia*, of the tribe Dissochaeteae, in some few Miconieae namely, in *Calophysa, Octopleura,* and *Sagraea,* in the genera *Rectomitra* and *Kibessia* of the Astronieae, and lastly, in *Memecylon* and *Mouriria* of the Memecyleae.

The structure of the cork-cells varies. Van Tieghem describes cork-cells with one-sided thickenings on the inner tangential walls in *Astronia, Dichaetanthera, Henriettea,* and *Mouriria.* In many cases the cork is homogeneous, i.e. composed of cork-cells of uniform nature, e.g. in *Dissotis.* In others the cork consists of alternating layers of flat and high quadrangular cells, as seen in a transverse section of the branch, e.g. in *Barbeyastrum,* in many Osbeckieae, in Tibouchineae (*Comolia, Heeria, Marcetia, Pterolepis, Tibouchina*) and Microlicieae (*Microlicia, Lavoisiera*).

In connexion with cork-formation, we may mention the occurrence of aerenchyma in a few marsh-plants, as described by H. Schenck, namely in *Rhynchanthera dichotoma,* DC., *R. cordata,* DC., and *Acisanthera variabilis,* Triana.

This tissue, which, as is well known, is homologous with the cork as regards its origin, consists of unsuberized cells with delicate walls, and by virtue of its intercellular spaces functions as a reservoir of air. It is found on the submerged portions of the stem and the older roots of the plants named; it takes its origin in the pericycle.

The primary cortex presents no special anatomical features. The following points alone require notice: the frequent occurrence in this tissue of stone-cells or of groups of these elements (e.g. in *Adelobotrys, Axinaea, Barthea, Blakea, Blastus, Centronia, Graffenrieda, Huberia, Meriania, Myriaspora egensis, Ossaea bracteata, O. microphylla, Oxyspora, Pachyanthus oleaefolius, Pachycentria constricta, P. tuberculata, Pogonanthera pulverulenta, Tetrazygia villosa*) and the presence of a ring of stone-cells, which is likewise not uncommon (e.g. in *Conostegia speciosa, Dissochaeta superba, Marumia muscosa, M. nemorosa, Mecranium haemanthum, Myriaspora decipiens, Omphalopus fallax*). The sclerenchymatous cells of the cortex just referred to are occasionally not thickened on all sides, but only in the form of a U.

The inner boundary of the primary cortex is formed by an endodermis, which is usually well marked. A composite and continuous sclerenchymatous ring, which frequently occurs at the outer limit of the bast in other Orders, has not been observed in any member of the Melastomaceae. Regarding the usual structure of the endodermis in the Order, Van Tieghem says: 'L'endoderme . . . est habituellement formé de cellules plates à parois minces et munies latéralement de plissements lignifiés.' *Macrocentrum cristatum* is characterized by an endodermis with cells of considerable size. Cells with thin walls are common, more rarely the endodermis is composed of cells thickened on all sides (*Allomorphia*), or cells thickened in the form of a U (*Anerincleistus, Calophysa, Dichaetanthera, Kibessia, Memecylon, Mouriria, Rectomitra*). On the inner side of the endodermis the pericycle first follows and then the bast-tissue. The pericycle consists of a varying number of layers of cells. It sometimes (*Blakea*, species of *Henriettella*, species of *Loreya, Kibessia, Memecylon, Plethiandra, Topobea*) contains a few bast-fibres; in *Creochiton* cells thickened in the form of a U are present; in *Calyptrella, Centronia*, and *Meriania* the pericycle is differentiated as sclerenchyma. There is nothing special to remark concerning the secondary bast.

As regards the crystalline elements in the axis we may refer to the statements in the section on the leaf-structure.

The **pith** consists of unlignified or lignified cells and frequently includes stone-cells or occasionally (*Topobea*) scattered fibrous cells.

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LYTHRARIEAE.

1. Review of the Anatomical Features. This Order is distinguished by the bicollateral structure of the vascular bundles. The following features are characteristic: (1) as regards the structure of the wood: the narrow medullary rays, the vessels with simple perforations and the wood-prosenchyma which bears simple pits and is septate, in the cases investigated; (2) as regards the structure of the cortex: the lack of a continuous sclerenchymatous ring, and the internal development of the cork (*Olinia* excepted, in which the cork-cambium arises subepidermally); in most cases it is formed in a pericyclic layer situated on the inner side of isolated groups of bast-fibres, rarely (*Lafoensia*) in the middle of the primary cortex. A definite type of stoma is wanting; the stomata are surrounded by a varied number of ordinary epidermal cells, which are not orientated in any special way. The occurrence of mucilaginous epidermal cells in the leaf is a very widely spread phenomenon in the Order; more rarely (*Sonneratia*) mucilaginous cells also occur in the mesophyll. Apart from these, secretory receptacles are absent, except in *Heteropyxis* and *Cuphea anagalloidea*, St. Hil., where secretory cavities occur. Oxalate of lime is usually excreted in the form of clustered and solitary crystals; the clustered crystals as a rule predominate. Styloids are of isolated occurrence (*Crypteronia*). The hairy covering (Fig. 80) is varied; there are simple unicellular or uniseriate hairs, tufted hairs (*Lagerstroemia*), shaggy hairs with a purely mechanical function or with a glandular head or base (*Cuphea*); spherical glandular hairs, which are sunk in pits on the lower side of the leaf and contain an intercellular space filled with secretion, are present in *Adenaria*, *Grislea*, and *Woodfordia*. In conclusion we may refer to the following points as special features, which may be utilized for detailed anatomical diagnosis: hypoderm in the leaf (*Crypteronia*); cuticular ridges on the epidermis of the leaf (*Duabanga*); papillose epidermis on the lower side of the leaf (*Duabanga*); branched spicular cells in the mesophyll and cortical parenchyma (*Sonneratia*); medullary groups of prosenchymatous cells (*Crypteronia*, *Duabanga*, *Sonneratia*); groups of thin-walled unlignified sacs, concentrically arranged in the wood and containing solitary crystals (*Olinia*); islands of soft bast in the wood of the root (*Lythrum*); formation of aërenchyma.

2. Structure of the Leaf. A comprehensive investigation of the leaf-structure has not yet been carried out. The following account is chiefly based on my own casual investigation of *Ammania latifolia*, L., *Woodfordia floribunda*, Salisb., var. β *glabrata*, *Lythrum Salicaria*, L., *Lafoensia punicaefolia*, DC., *Crypteronia glabra*, Endl., *Lagerstroemia floribunda*, Jack, and *Olinia cymosa*, Thunb., as well as on Niedenzu's statements regarding the leaf-structure of the three genera classed together by him as the Order Blattiaceae, viz. *Sonneratia* (=*Blatti* in Niedenzu's work), *Duabanga* and *Crypteronia*, and also of the genus *Punica*, which is regarded as forming a separate Order—Puniceae.

The leaf-structure is bifacial or centric. A special type of **stoma** is wanting; the pair of guard-cells is surrounded by an indefinite number of irregularly orientated, ordinary epidermal cells. Not uncommonly the stomata occur on both sides of the leaf, e.g. in *Lythrum Salicaria* and *Sonneratia acida*, L. f. In the species last mentioned the stomata are deeply depressed. The occurrence of mucilaginous epidermal cells is very widely distributed. Radlkofer mentioned their presence in *Peplis Portula* and *Lythrum Salicaria* in his first publication on mucilaginous epidermal cells (Monogr. von *Serjania*, 1875). Then followed Bokorny's statement as to the presence of mucilaginous cells in both upper and lower epidermis in *Ammannia glauca*, Wall., *Cuphea anagalloidea*, St. Hil., and *Diplusodon ovatus*, Pohl; I have likewise found them in the species of

Ammannia, *Lafoensia*, *Lagerstroemia*, and *Woodfordia* mentioned above. A somewhat collenchymatous hypoderm consisting of one layer is developed on the upper side of the leaf in *Crypteronia glabra*. Cuticular ridges are found on the upper side of the leaf in *Duabanga*; in the same genus the epidermal cells on the lower side of the leaf are produced into long mammilliform papillae. In *Sonneratia*, according to Schimper, the middle of the leaf is occupied by thin-walled colourless aqueous tissue, in which branched sclerenchymatous cells (spicular cells) occur, while the assimilatory tissue contains numerous large mucilage-cells. Special **secretory receptacles** are wanting in most members of the Order. The only exceptions are afforded by *Cuphea anagalloidea*, St. Hil.

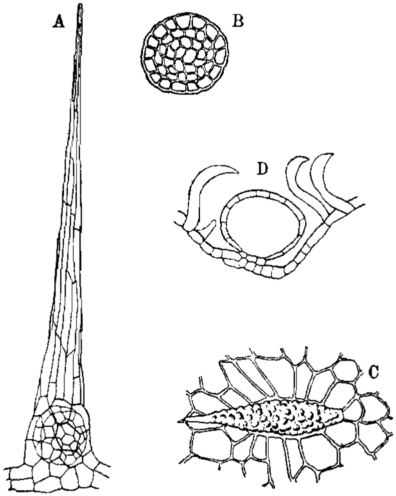

FIG. 80. Forms of trichomes of the Lythrarieae. A, B, Shaggy hair of *Cuphea lanceolata* with glandular base; the latter cut transversely in B. C, Trichome of *Cuphea appendiculata*, Benth. D, Section of an external gland of *Woodfordia floribunda*, Salisb.—A, B, after Martinet, C, D, Original.

(but not by the closely related species, *C. pascuorum*, Mart.) and the anomalous genus *Heteropyxis*, in both of which secretory cavities occur; these are provided with an epithelium in the first species, but in *Heteropyxis* they arise lysigenously (according to Engler). The cavities give rise to transparent dots in the leaf. In the leaf, and also in the axis, **oxalate of lime** is, as a rule, differentiated in the form of clustered crystals. In most members of the Order investigated by me and cited above, clustered crystals occur abundantly in the veins; only now and then a solitary crystal replaces a clustered crystal. *Lagerstroemia floribunda* and *Olinia cymosa* are exceptional, in having solitary crystals, which are present in unusual abundance, and are situated in the veins in the first species,

in the bast of the branch in the other species. Idioblasts, occupied by solitary crystals, are found in the mesophyll of *Punica Granatum*; styloids occur in the inner and outer phloem of the axis of *Crypteronia*, while in the leaf there are only clustered crystals. We may now describe the **hairy covering**. Firstly, simple, conical, one or two-celled hairs occur in *Lythrum Salicaria*. I have met with simple, few-celled, uniseriate hairs in *Woodfordia*, and tufted hairs with a short uniseriate stalk on the branches of *Lagerstroemia floribunda*. Shaggy hairs of two forms were observed in *Cuphea*; they are either simply mechanical, consisting of fairly thick-walled cells, e.g. in *Cuphea appendiculata*, Benth., or they have a glandular function, the hair being composed of thin-walled cells and surmounted by a multicellular glandular head (*Cuphea anagalloidea*, St. Hil., and *C. pascuorum*, Mart.). With the latter type we may class the long, conical, multiseriate, shaggy hairs (Fig. 80, *A–B*), observed by Martinet in *Cuphea lanceolata*, and recalling the well-known glandular shaggy hairs of *Dictamnus*; they consist of elongated cells and their basal portion encloses a central glandular group of numerous small isodiametric cells. The species *Cuphea appendiculata* mentioned above also possesses simple unicellular hairs (Fig. 80, *C*) of a characteristic type; they are placed obliquely or almost parallel to the surface of the leaf and arise from an epidermal cell which appears elliptical in surface-view; they sometimes show a tendency to differentiation into a two-armed form, and possess a strongly thickened silicified membrane furnished with small knobs or warts. Finally, we may mention the black glandular dots, which Bentham and Hooker and others have described as occurring on the lower side of the leaf in the three genera *Adenaria*, *Grislea*, and *Woodfordia* [1]. I have been able to examine them in *Woodfordia floribunda*, Salisb. and *Adenaria floribunda*, H. B. K., and have found that they are due to sessile, spherical, glandular hairs (Fig. 80, *D*), which are sunk in pits on the lower side of the leaf. The wall of these hairs consists of a single layer of flat cells, possessing a polygonal outline in surface-view; internal to this there is a large intercellular secretory space.

3. STRUCTURE OF THE AXIS. Since the discovery (made almost simultaneously by Sanio and Dr. Fr. Schreiber) of the bicollateral structure of the vascular bundles in the Lythrarieae (especially in *Lythrum Salicaria*), a considerable number of species have been investigated, and **intraxylary soft bast** has been met with in all cases: e.g. by Petersen in species of *Cuphea*, *Ammannia*, *Peplis* [2], *Lagerstroemia*, *Lawsonia*, *Nesaea*, and *Punica*, by me in species of *Lagerstroemia*, *Lafoensia*, and *Olinia*, and by Niedenzu in the Blattiaceous genera *Sonneratia*, *Duabanga*, and *Crypteronia*. The differentiation of this tissue in the individual species exhibits little variation, but it may be noted that the inner soft bast occasionally (e.g. in *Lagerstroemia indica*) grows in thickness by means of a cambium.

With regard to the structure of the **pith** we may specially point out the occurrence of groups of prosenchymatous cells (mentioned by Niedenzu) in the pith, in the genera of Blattiaceae. These groups are specially clear in *Duabanga*; in *Sonneratia* they are less distinct on account of the thinness of their cell-walls; in *Crypteronia* they have very thick walls and are frequently scattered, but often also occur in bundles. The pith of *Punica Granatum* is reticulately heterogeneous (Mentovich).

The following remarks on the structure of the **wood** are chiefly based on my investigation of species of the genera *Lagerstroemia*, *Lafoensia*, *Olinia*, and

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[1] According to Köhne (Monogr. der Lythrarieae, in Engler's Bot. Jahrb.) dots of this kind also occur in *Lagerstroemia madagascariensis*, Bak. and *L. punctata*, Bl.; the inclusion of these species in the genus *Lagerstroemia* thus requires further consideration.

[2] In *Peplis Portula*, according to H. Schenck, in the land-form as well as in the water-form.

Punica. The medullary rays are narrow and only uni- or bi-seriate (also in *Lythrum Salicaria*, according to Herbst, and in the Blattiaceae, according to Niedenzu). The lumina of the vessels vary in width (maximum diameter = ·066–·15 mm.); their perforations are simple, circular or elliptical (also in the Blattiaceae, according to Niedenzu). In contact with parenchyma of the medullary rays the walls of the vessels either bear bordered (*Crypteronia, Lafoensia, Olinia, Punica*), or simple pits (*Lagerstroemia*). The wood-prosenchyma has simple pits; thin division-walls were observed in these elements in the species of the four genera I examined. The wood of *Olinia* presents a specially noteworthy feature, as it includes unlignified groups of parenchymatous cells containing solitary crystals and arranged concentrically.

The following account of the structure of the **cortex** is based on my own investigation of *Lafoensia punicaefolia, Lagerstroemia floribunda, Olinia cymosa*, and *Punica Granatum*, as well as on the statements in the literature.

In *Sonneratia* and *Olinia* the primary cortex contains spicular cells. In *Olinia cymosa* they are elongated like short fibres: they have more or less thick walls with corresponding variation in the width of the lumina, and are only slightly branched. Cortical vascular bundles are wanting; epidermis and primary cortex are alone concerned in the formation of the four narrow wings which are found on the young branches of *Duabanga, Crypteronia Cumingii*, Planch., and *Punica*.

The outer portion of the pericycle usually contains isolated groups of bast-fibres (*Cuphea, Lafoensia, Lagerstroemia, Lythrum, Punica*, &c.); more rarely (*Olinia*, &c.) these are wanting, and are sometimes (*Peplis*) replaced by an endodermis.

Development of cork usually takes place in the inner parenchymatous part of the pericycle (in *Lagerstroemia floribunda* and *Punica Granatum*, and also in species of *Ammannia, Lagerstroemia, Lawsonia, Lythrum*, and *Nesaea*, according to Petersen). An exception to this is afforded by *Lafoensia punicaefolia*, in which the cork-cambium arises in the middle of the primary cortex, and by *Olinia cymosa*, in which the subepidermal cell-layer becomes the phellogen. In *Lafoensia punicaefolia* the cork-cells have wide lumina and thin walls; in *Lagerstroemia floribunda* pitted cells thickened in the form of a U and in *Punica* cells with sclerosed inner tangential walls occur in the cork-tissue. Formation of aërenchyma has been observed by H. Schenck in *Lythrum Salicaria*, L., *L. virgatum*, L., *Cuphea aperta*, Köhne, *C. Balsamona*, Cham. et Schlecht., *C. ingrata*, Cham. et Schlecht., and in *Heimia myrtifolia*, Cham. et Schlecht. In the cases specially investigated the development of the aërenchyma is pericyclic.

The secondary bast contains: bast-fibres in *Lagerstroemia* and *Lafoensia*; large stone-cells and sacs containing clustered crystals in *Punica Granatum*, the latter elements being arranged in concentric circles; styloids and sclerenchymatous cells, the latter elongated like bast-fibres and having numerous pits, in *Crypteronia*; numerous chambered fibres with solitary crystals in *Olinia*.

4. **Structure of the root.** The following features are of special interest: (1) the occurrence (described by Frémont) of islands of soft bast in the wood of the root of *Lythrum Salicaria*; they are given off by the cambium on its inner side; and (2) the structure of the respiratory roots of *Sonneratia*, which rise up perpendicularly from the mud of the mangrove-region and may attain a length of 1½ metres and a thickness of 4 cm. According to Goebel they are covered by a number of thin cork-lamellae, which are superposed and consist of three cell-layers each. The cells of the outermost layer have their walls rounded off externally, and are not suberized; the cells of the middle layer are tabular and suberized; those of the innermost layer are elongated in the radial direction, rounded off internally and suberized. Between each pair of cork-lamellae there are one, two or several layers of approximately spherical cells, so that a separation of the cork-lamellae can take place

at these points. The cortex of the root of *Sonneratia*, like the mesophyll and the cortex of the stem, contains spicular cells, the pointed prolongations of which project into the intercellular spaces.

Literature: [Desmoulins, Anat. du genre *Schufia*, Bordeaux, 1862, 64 pp.]—Martinet, Org. de sécrétion, Ann. sc. nat., sér. 5, t. xiv, 1872, p. 176 and pl. 16.—Radlkofer, Monogr. von *Serjania*, 1875, p. 104.—Möller, Holzanat., in Denkschr. Wiener Akad. 1876, pp. 103, 104 and 399.—Bokorny, in Flora 1882, p. 380 and separate copy, pp. 34, 35.—Möller, Rindenanat., 1882, p. 353.—Petersen, in Engler, Bot. Jahrb., Bd. iii, 1882, pp. 369, 370.—[Briosi, Foglie e l'embrione delle *Cuphea*, Roma, 1882.]—Mentovich, Pflanzl. Mark, Klausenburg, 1885, Hungarian; abstr. in Just 1885, i, p. 789.—Solereder, Holzstr., 1885, pp. 136, 137.—Göbel, Luftwurzeln v. *Sonneratia*, in Ber. deutsch. bot. Gesellsch. 1886, pp. 249-55.—H. Schenck, Vergl. Anat. d. submers. Gew., Cassel, 1886, p. 32 and Tab. v.—Petit, Pétiole, Mém. Soc. sc. phys. et nat. de Bordeaux, sér. 3, t. iii, 1887, p. 316.—Schenck, Aërenchym, Pringsheim Jahrb., Bd. xx, 1889, pp. 543-7.—Frémont, Tubes criblés extralibériens de la racine des *Lythrum*, Journ. de bot. 1891, p. 448.—Schimper, Indo-malay. Strandfl., Jena, 1891, p. 16 and Tab. iv.—Chodat, in Rep. Congress Genoa 1892, p. 147.—Köhne, in Natürl. Pflanzenfam., iii. Teil, Abt. 7, 1892, p. 2.—Niedenzu, loc. cit., pp. 17 and 23.—Gilg, in natürl. Pflanzenfam., iv. Teil, Abt. 3 a, 1894, p. 214.—Herbst, Markstr., Bot. Centralbl. 1894, i, p. 354.—Bonbier, Infloresc. des *Cuphea alterniflora*, Bull. Herbier Boissier, t. iv, 1896, pp. 328-335.—Wittlin, Kalkoxalattaschen, Bot. Centralbl. 1896, iii, p. 100.—Engler, in Natürl. Pflanzenfam., Nachtr. u. Reg., Teil ii-iv, 1897, p. 335.—[Schrenk, Float. tissue of *Nesaea*, Bull. Torrey bot. Club 1889, pp. 315-23, 3 Tab.]

ONAGRARIEAE.

This Order is characterized anatomically by: the presence of intraxylary phloem, the occurrence of bundles of raphides (exception: *Trapa*), the lack of a special type of stoma, the lack of both internal and external glands, the simple perforations of the vessels, the wood-prosenchyma bearing simple pits, and the development of the cork, which takes place deep in the interior of the branch.

The structure of the leaf and axis have been investigated chiefly by Parmentier[1]. The following points may be mentioned with regard to the former. The **mesophyll** either shows a differentiation into palisade and spongy tissue, while its structure varies from bifacial to centric, or it consists of a homogeneous loose parenchymatous tissue. The **stomata** are surrounded by three or more epidermal cells and follow the Ranunculaceous or Cruciferous type. They occur either on both surfaces of the leaf, or only on the lower side, while in *Trapa*, and, curiously enough, according to Diels, also in *Epilobium crassum*, Hook. f.[2], they are found only on the upper side. I have met with mucilaginous **epidermal cells**[3] in *Jussiaea erecta*, L., *J. repens*, L., and *J. natans*, H. et B., and in *Trapa natans*, L. **Raphides** are stated by Parmentier to occur in the genera *Epilobium*, *Zauschneria*, *Jussiaea*, *Ludwigia*, *Gayophytum*, *Clarkia*, *Oenothera*, *Fuchsia*, *Hauya*, *Lopezia*, *Gaura*, *Gongylocarpus*, and *Circaea*. In addition to the raphides, clustered crystals are present in *Jussiaea* and *Ludwigia*, and styloids in *Hauya elegans* (in the pith, bast, and leaf-tissue); only clustered crystals occur in *Trapa*, chiefly in small cells arranged in groups and projecting, as small round bladders with a broad base, into the intercellular spaces, with which *Trapa*, like other water-plants, is provided. In the genera investigated by Parmentier, the **hairy covering** consists, in almost all cases, solely of simple unicellular hairs of varied shape; the club-shaped unicellular trichomes present in many genera are specially worthy of notice. Uniseriate hairs, consisting of few cells, have been

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[1] Parmentier's work extends to the genera *Epilobium*, *Zauschneria*, *Jussiaea*, *Ludwigia*, *Clarkia*, *Gayophytum*, *Oenothera*, *Fuchsia*, *Hauya*, *Lopezia*, *Gaura*, *Gongylocarpus*, *Circaea*, and *Trapa*.

[2] The leaf of *E. crassum* has bifacial structure with palisade-tissue above and colourless parenchyma with raphide-sacs below; hence the abnormal position of the stomata.

[3] These are the 'cellules flotteurs,' which Parmentier described in species of *Jussiaea* and *Trapa*; they were, however, incorrectly interpreted by him.

met with only in species of *Fuchsia, Jussiaea,* and *Ludwigia*; in *Trapa*; they are multicellular. Glandular hairs are wanting. The interior of the secretory leaf-teeth in species of *Epilobium* and *Fuchsia* consists of the termination of a vein, with an epithema which, in *Fuchsia*, at any rate, must be regarded as modified wood-parenchyma, while at the apex of the tooth there is a large water-pore; in *Fuchsia* they are hydathodes (Reinke, Haberlandt).

According to Petit, the **petiole** contains a single arc-shaped vascular bundle in the initial region. The characteristic region is similarly constituted, or possesses two small additional lateral bundles.

Intraxylary phloem, mentioned above in the diagnosis of the Order, has

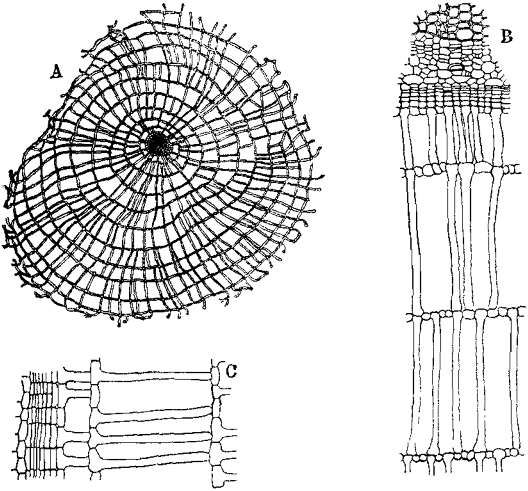

FIG. 81. A, Cross-section through an aerial root of *Jussiaea repens*. B, C, *Jussiaea peruviana*, L.: B, cross-section; C, radial longitudinal section of the aërenchyma.—A, after Goebel, B, C, after H. Schenck.

been demonstrated by different authors (Sanio, Petersen, Rützou, J. E. Weiss, Solereder, Parmentier) in numerous species belonging to the genera *Epilobium, Zauschneria, Jussiaea, Ludwigia, Clarkia, Gayophytum, Oenothera, Eucharidium, Fuchsia, Hauya, Lopezia, Gaura, Gongylocarpus, Circaea,* and *Trapa*. It shows varied differentiation, for it may either closely adjoin the system of vascular bundles, or appear in the form of small medullary groups.

In *Oenothera odorata* the inner soft bast unites to form an almost continuous ring at an early stage. In other Onagrarieae isolated bundles of phloem appear, and are situated immediately adjoining the inner margin of the wood. In *Oenothera riparia* only a certain number of these isolated phloem-bundles give the impression of belonging to the fibro-vascular system; others appear to be embedded in

the outer part of the pith. In *Chamaenerium angustifolium* small phloem-groups occur immediately internal to the spiral tracheae of the vascular ring and actually belong to the vascular bundles; but within these there is another zone of groups of soft bast, separated from the first by several layers of cells having the same character as the cells of the pith. Lastly, *Jussiaea acuminata* and *J. octonervia* as well as *Ludwigia alternifolia* possess true medullary groups of soft bast; in *Jussiaea* they are very small, and frequently smaller in circumference than a pith-cell.

In this Order (*Fuchsia fulgens*, Moç. et Sesse, *F. macrostemma*, Ruiz et Pav.; *Jussiaea erecta*, L.) a transverse section of the **wood** shows narrow, uni- or bi-seriate medullary rays[1] and vessels with fairly large lumina (in *Fuchsia* attaining ·084 mm. in diameter). The bordered pits of the vessel-walls have the sieve-plate-like structure discovered by Bengt Jönsson (*Fuchsia*, *Jussiaea*). In most cases simple pits are found on the wall of the vessel where it is in contact with parenchyma of the medullary rays. The perforations of the vessels are simple. The wood-prosenchyma has wide lumina and simple pits: in *Fuchsia* it is septate.

In the structure of the **cortex** the nature of the pericycle and the origin of the cork are of systematic importance. The pericycle, as a rule (*Circaea*, *Clarkia*, *Epilobium*, *Fuchsia*, *Gaura*, *Gayophytum*, *Godetia*, *Gongylocarpus*, *Jussiaea*, *Lopezia*, *Ludwigia*, *Oenothera*, *Zauschneria*), contains isolated groups of bast-fibres, which occasionally become united into an almost continuous ring; in *Isnardia palustris*, a pronounced aquatic type with a thick and very lacunar cortex, there is a suberized endodermis. The cork arises on the inner side of the pericyclic groups of bast-fibres (*Clarkia*, &c.). In Onagrarieae inhabiting marshes, aërenchyma, which is often strongly developed, is produced by the phellogen in place of cork. This aërenchyma was first described by Martins in *Jussiaea* and subsequently by H. Schenck in numerous species of *Jussiaea*, *Oocarpon jussiaeoides*, Micheli, *Epilobium roseum*, Retz., and *E. palustre*, L. It occurs not only on the submerged portions of the stem, but also on the roots, and is specially well-marked in the aerotropic roots of *Jussiaea repens*, L. (Fig. 81), &c.

The primary cortex is lacunar in species of *Fuchsia*, *Jussiaea*, *Ludwigia*, and *Oenothera* (as well as in *Isnardia*), and especially so in *Trapa*. According to Parmentier, the **bast** sometimes contains stone-cells in *Hauya* and bast-fibres in *Fuchsia*. In *Trapa* the pith has large intercellular spaces; in many members of the Order, a partial resorption of this tissue takes place, while it is persistent in others (*Hauya*).

In some Onagrarieae **interxylary phloem** occurs in the wood of the stem or root. Ramaley demonstrated it in stems of a certain thickness in *Oenothera biennis*, L., *O. missouriensis*, Sims., *O. pallida*, Lindl., *O. rhombipetala*, Nutt., and *O. sinuata*, L.; J. E. Weiss found it in the roots of *Oenothera biennis* and species of *Gaura*, and Frémont also in the roots of *Oenothera cruciata*, *O. Fraseri*, *O. macrocarpa*, *O. parviflora*, and *O. Sellowi*. With regard to the species investigated by him, J. E. Weiss showed that the innermost islands of soft bast in the wood of the root are the continuations of the intraxylary phloem-strands of the stem, while the remainder are given off by the cambium on its inner side. Finally, in *Oenothera Fraseri* and *O. riparia*, according to Frémont, we meet with the rare occurrence of **intraxylary phloem** in the root. According to Frémont, this is also found in *Epilobium parviflorum*, but here the pith only arises at a late stage by dilatation, and the intraxylary phloem is likewise only developed secondarily.

Literature: [Barnéoud, Mém. sur l'anat. et l'org. du *Trapa natans*, Paris, 1848.]—[Martins, Racines aërifères etc. du genre *Jussiaea*, Mém. Acad. sc. de Montpellier 1866.]—Chalon, Tiges

[1] *Epilobium boreale*, 'W.' and *Oenothera muricata* possess similar rays according to Herbst.

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SAMYDACEAE.

1. Review of the Anatomical Features. According to the results of the investigations hitherto undertaken, which are only of a preliminary nature, the following features may be pointed out as general characteristics of the Order: the superficial origin of the cork, the tendency to the formation of scalariform perforations in the vessels, the wood-prosenchyma with simple pits and often septate, the lack of glandular hairs and the occurrence of a characteristic type of stoma (subsidiary cells parallel to the pore). It may be added that the perforations of the vessels are, as a rule, simple, but in the neighbourhood of the primary or even in the secondary wood scalariform perforations with few bars are met with, though they are less numerous than those of the other type; in *Osmelia* exclusively scalariform perforations have been observed. The outer limit of the bast is occupied by isolated bundles of hard bast or by a composite and continuous sclerenchymatous ring. Schizogenous secretory cavities are present only in the tribe Casearieae, *viz.* in *Samyda*, *Euceraea*, *Casearia* pro parte, *Lunania* pro parte, and *Osmelia* pro parte; they frequently give rise to transparent dots or striae on the leaves. The hairy covering consists of simple, unicellular sclerenchymatous hairs, of stellate hairs (species of *Abatia* and *Casearia*) or of unicellular malpighian hairs (*Homalium racemosum*, Jacq.). Oxalate of lime is excreted in the form of clustered and solitary crystals. Important characters for specific diagnosis are the occurrence in the leaf of a many-layered epidermis (species of *Abatia* and *Asteropeia*) and of epidermal cells containing small clustered crystals (species of *Homalium* and *Samyda*).

2. Structure of the Leaf. An exhaustive work on the structure of the leaf is still wanting. The account given here is based on my own investigation of *Samyda serrulata*, L., *Casearia grandiflora*, Camb., *Homalium racemosum*, Jacq., *Banara guianensis*, Aubl., and *Abatia tomentosa*, Mart., and on the scattered statements in the literature. In the five species just quoted belonging to the different tribes of the Order, the **stomata** always occur only on the lower side of the leaf; the guard-cells are relatively small and are destitute of special eisodial ridges; they are always accompanied by neighbouring cells, parallel to the pore, which occasionally appear as distinct subsidiary cells in consequence of their shape being different from that of the other epidermal cells. The anomalous genus *Asteropeia*, however, forms an exception, the stomata being surrounded by several subsidiary cells in a rosette. The

hairy covering in most cases consists of unicellular sclerenchymatous hairs of varied length (*Samyda serrulata; Abatia tomentosa, A. americana*, Eichl., *A. microphylla*, Taub.). According to Harms, *Abatia verbascifolia*, Ruiz et Pav., possesses stellate hairs; these also occur in *Casearia grandiflora*, according to my own investigation, two or three short unicellular sclerenchymatous hairs being sunk side by side in the epidermis of the leaf. I have met with transitions from ordinary hairs to true malpighian hairs in *Homalium racemosum*; in the first place, quite short and pointed sclerenchymatous, unicellular hairs occur in this plant; somewhat longer hairs of the same kind show transitions to the two-armed hairs, which are likewise sclerenchymatous and unicellular and are mostly provided with arms of unequal length. Glandular hairs are completely absent in the Order. **Oxalate of lime** is excreted in the form of clustered and solitary crystals. Occasionally, clustered crystals are found in the epidermis; the cells containing them are distinguished from the rest of the epidermal cells by the small size of their lumina, and are combined to form groups (*Samyda serrulata, Homalium racemosum*). **Secretory elements** have only been met with in the tribe Casearieae. Their character is generally that of secretory cavities, and they frequently give rise to transparent dots or small striae in the leaf. In those cases which I have seen, they have a distinct but delicate one-layered epithelium, and hence they are probably of schizogenous origin. They are found in all the species of *Samyda* hitherto investigated (Bokorny and Warburg), as well as in the monotypic genus *Euceraea* with *E. nitida*, Mart. (according to Bokorny [1]). Secretory cavities only occur in a certain number of the species of the genera *Casearia* (according to Eichler, Bokorny, Harms, &c.), *Lunania* (according to Warburg), and *Osmelia* (according to Warburg). As regards the genus *Casearia*, Bokorny was unable to find a trace of resin-cavities in *C. Commersoniana*, Camb., nor did Harms meet with any in *C. Commersoniana, C. javitensis*, H. B. K., and *C. laurifolia*, Benth.; this is in agreement with the fact that both Eichler in Flora brasiliensis XIII, 1, 1871, pp. 458, 461, and 483, and Bentham and Hooker in Genera Plantarum, I, 1867, p. 797, had previously stated that transparent dots (caused by the secretory cavities) were absent in all the species of *Casearia* belonging to the section *Piparea*, to which the species mentioned above belong. Moreover, according to Eichler, the transparent dots are also wanting in individual species of the sections *Pitumba* and *Crateria*, sometimes even in certain specimens of species which normally possess dots (e. g. *C. inaequilatera*, Camb.); it remains to be determined whether the secretory cavities may not be really present in these plants, though they do not give rise to transparent dots. We may also draw attention to the fact that the secretory cavities are occasionally met with in the branch. According to Van Tieghem, they are found in the cortex and pith (*Samyda procera*), or in the cortex only (*Samyda suaveolens*); in *Casearia grandiflora* I have observed them in the bast and primary cortex. In some members of the Order the cortex of the branch, according to Van Tieghem, only contains isolated secretory cells in place of the secretory cavities which occur in the mesophyll (*Casearia inaequilatera, C. resinifera*).

There is little to be said concerning the remaining anatomical features of the leaf, as only a small number of species have been investigated. It perhaps deserves notice that the vascular bundles of the **veins**, in the cases investigated, are provided with sclerenchyma, and that the smaller veins are either embedded (*Casearia grandiflora, Abatia tomentosa*), or vertically transcurrent (*Samyda serrulata*). The **epidermis** on the upper side of the leaf is described by Harms as composed of four layers in *Asteropeia*, two layers in *Abatia americana*

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[1] Bokorny's statement, which Warburg regarded as requiring further examination, is quite correct, as the investigation I have recently undertaken has shown.

and *A. microphylla*, and locally of two layers in *Abatia verbascifolia* and *A. tomentosa*. In *Asteropeia amblyocarpa*, Tul., which I have examined, there is a three-layered hypoderm beneath the epidermis on each side of the leaf; the uppermost cell-layer of this hypoderm consists of cells as small as those of the epidermis, and in places includes stone-cells, while the inner two layers have cells with wide lumina, filled with brown contents (in the dried leaf).

3. STRUCTURE OF THE AXIS[1]. The formation of cork is superficial. In *Casearia grandiflora*, *Homalium racemosum*, and *Abatia tomentosa* the cork arises in the outermost cell-layer of the primary **cortex**. In *Samyda serrulata* and *Abatia tomentosa* the cork-cells have fairly wide lumina; in *Casearia grandiflora*, *Homalium racemosum*, and *Banara guianensis* they are thickened on one side. The outer limit of the bast is formed by isolated groups of bast-fibres (*Abatia*), by isolated groups of bast-fibres supplemented by stone-cells (*Banara guianensis*), or by a closed and composite sclerenchymatous ring (species of *Banara* and *Poliothyrsis sinensis*, Benth. according to Harms, *Samyda serrulata*, *Casearia grandiflora*, *Homalium racemosum*).

In transverse section the **wood** shows medullary rays which are usually from one to three cells, rarely (*Poggea alata*, Gürke, according to Harms) as much as five cells in breadth, and vessels with lumina of varied size (maximum diameter = ·03 mm. in *Samyda*, ·06 mm. in *Casearia* and *Banara*). The perforations of the vessels exhibit a tendency to scalariform differentiation. They are usually simple, but accompanying this type scalariform perforations (with 5–8 bars) occur in the primary wood in: *Banara parviflora*, Benth., *B. brasiliensis*, Benth., *Homalium fagifolium*, Benth., *H. involucratum*, O. Hoff., *H. racemosum*, Jacq., *H. pedicellatum*, Benth., *Bivinia Jaubertia*, Tul., *Poliothyrsis sinensis*, Benth., according to Harms' observations; and likewise in *Samyda serrulata*, *Casearia grandiflora*, *Banara guianensis*. Scalariform perforations (with few bars) have also been met with in the secondary wood accompanying the more frequent simple perforations in *Casearia Selloana*, Eichl. and *Poggea alata*, Gürke, as well as in species of *Abatia* by Harms, and similarly by me in *Homalium racemosum*. According to Harms, the vessels of *Osmelia conferta*, Benth., have exclusively scalariform perforations. Simple perforations only are stated by Harms to occur in *Asteropeia*. Spiral thickening of the vessel-wall has been observed in *Abatia tomentosa* and in the species of the same genus investigated by Harms (*A. americana*, *A. microphylla*, *A. verbascifolia*), and likewise in *Poliothyrsis sinensis*. In contact with parenchyma of the medullary rays, distinct (*Samyda*, *Casearia*, *Homalium*) or somewhat indistinct (*Banara*, *Abatia*) unilateral bordered pits occur on the vessel-wall. The wood-parenchyma does not take a prominent part in the formation of the wood. The wood-prosenchyma in the cases investigated has thick walls, but never very narrow lumina, and bears simple pits. Delicate division-walls were occasionally met with in the lumina of the wood-prosenchyma in the species of *Samyda*, *Casearia*, *Homalium*, *Banara*, and *Abatia*.

Literature: Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 74 and 370.—Bokorny, Durchs. P., Flora 1882, p. 380 and separate copy, p. 34.—Solereder, Holzstr., 1885, p. 138.—Turner, Vergl. Anat. d. Bixac. etc., Diss., Göttingen, 1885.—Van Tieghem, in Ann. sc. nat., sér. 7, t. i, 1885, p. 59.—Radlkofer, in Sitz.-Ber. Münch. Akad. 1886, p. 318.—Harms, in Engler, Bot. Jahrb., Bd. xv, 1893, pp. 613–23.—Warburg, in Natürl. Pflanzenfam., iii. Teil, Abt. 6, 1893, pp. 3, 4.

[1] The structure of the axis was investigated by me in the same species as the leaf-structure.

LOASEAE.

The most mportant anatomical character of the Order is constituted by the **hairy covering** (Fig. 82), which has been investigated especially by Greinert and Gilg. Gilg describes the following typical forms of hairs as occurring in the Order (forms intermediate between these types are, however, frequently found): (1) Simple, unicellular hairs or bristles of variable length, with a wall which *may or may not be silicified*; (2) unicellular, very pointed, conical, and strongly silicified hairs, having their whole surface beset with sharp or blunt spines, which are directed forwards or backwards (Fig. 82, *D–G*); (3) unicellular, strongly silicified, barbed hairs of variable length and commonly comparable to a many-fluked anchor, the stalk being sometimes densely covered with spines, which are curved forwards or backwards (characteristic of almost all the Loaseae, Fig. 82, *A–C*); (4) long unicellular, hooked, or climbing hairs, with a

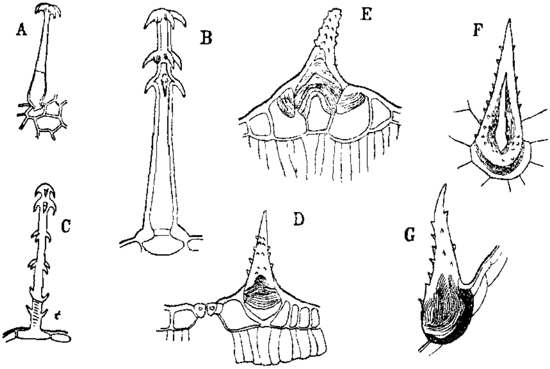

FIG. 82. Hairy covering of the Loaseae. A–C, Unicellular anchor-hairs. A, B, *Eucnide lobata*, Gray; C, *Cajophora lateritia*, Klotzsch. D, E, *Petalonyx Thurberi*, Gray: D, cystolith-hair; E, trichome with merely calcified, but strongly thickened wall, without a cystolith, but with cystoliths in the subsidiary cells. F, G, *Loasa chelidonifolia*, Benth.: F, cystolith hair adpressed to the leaf, back-view, G, in side-view.—Original.

high multicellular base, and bearing several sharp hooks at the apex; they show active protoplasmic movement; (5) long unicellular, slightly silicified, sickle-like hairs, without visible protoplasmic movement; (6) long unicellular, thinly filiform hairs, with local tuber-like swellings, and sharply attenuated at the apex or with barbs; (7) strongly silicified, unicellular stinging bristles, which are usually very long, and are often provided with a multicellular base; they frequently possess yellowish contents, which have a strongly irritating effect on the skin of animals, and become discharged into the wound formed by the bristle, when the slightly recurved blunt apex is broken off (characteristic of a large number of the Loaseae); (8) short, simple, multicellular hairs (of rare occurrence); (9) multicellular glandular hairs, provided with a uniseriate stalk of varied length and (according to Greinert) a unicellular head. In numerous species

hairs belonging to five or six of the forms just mentioned may be observed irregularly intermingled with one another.

Other essential characters, which Gilg does not refer to, are (*a*) the presence, in most of the types of hairs described, not only of silica but frequently of a large amount of lime as well, and (*b*) cystolith-like structures, for the most part strongly impregnated with carbonate of lime, and occurring in the unicellular hairs of the various types (with the exception of the stinging hairs) and in their subsidiary cells (sometimes also in the subsidiary cells of the stinging hairs). Kohl described cystolith-hairs as occurring in *Cajophora lateritia* (which, by the way, he quite incorrectly placed in the Cannabineae), as well as in *Gronovia scandens*. According to my own observations, these hairs are also found in *Petalonyx Thurberi*, Gray, *Mentzelia albescens*, Griseb., *Eucnide lobata*, Gray, *Loasa chelidonifolia*, Benth., and *Blumenbachia insignis*, Schrad., and are without doubt widely distributed throughout the Order. The mode of differentiation of the cystoliths within the cell of the hair varies. A distinct stalk is never present. In the conical hairs of *Petalonyx Thurberi*, Gray (Fig. 82, *D*), which bear solid forwardly directed spines, the body of the hair, so to speak, forms the stalk of the cystolith; the cystolith-body, which is attached to it, projects convexly into the lumen of the basal portion of the hair and is strongly incrusted with lime. In the verrucose conical hairs of *Loasa chelidonifolia* (Fig. 82, *F–G*), which are usually obliquely placed, the cystolith-body arises near the base of the hair on the more strongly thickened longitudinal side of its wall, and so on; the figures show further details. In addition to the cystoliths in the hair-cell, as has already been mentioned, similar structures also occur in the subsidiary cells of the hair (*Petalonyx Thurberi*, Fig. 82, *E*, *Mentzelia albescens*, *Eucnide lobata*, *Blumenbachia insignis*, and *Cajophora lateritia*, Klotzsch). The cystoliths of the subsidiary cells are flat structures, each of which is fused with the outer and with one lateral wall (viz. that adjoining the hair) of the cell bearing it. The subsidiary cells containing cystoliths are arranged in a single ring or in several rings around the hair; in the second case (*Eucnide lobata*) they are visible even to the naked eye as knobs or as ' false scales.' It may be added that the cell-walls of these rosettes of cystoliths are usually strongly silicified, and that sometimes the cystolith-bodies themselves are strongly silicified instead of being calcified. The occurrence of cystolith-hairs and structures resembling cystoliths in the Loaseae is of great systematic interest, for it sheds new light on the relationship of the Loaseae to the Cucurbitaceae, which likewise possess cystoliths, an affinity emphasized by some authors and denied by others.

The following statements may be added regarding the stinging hairs mentioned above. Their structure is generally the same as in the well-known stinging hairs of the nettle; here also a pedestal bearing the base of the stinging hair is frequently present. According to Haberlandt, the apex of the stinging hair in *Loasa papaverifolia* is simply curved and rounded off; in the region of fracture of the hair-tip, however, there are thin portions of the wall, similar to those in the stinging hairs of the nettle. Other members of the Order (species of *Loasa*, *Blumenbachia*, and *Cajophora*) show all transitions from ordinary capitate hair-tips (as in *Urtica*) to those of *Loasa papaverifolia*. The brittleness of the head necessary to insure its breaking off is not due to silicification, but to calcareous incrustation in that part of the wall. The poison of the stinging hairs has been recently described by Tassi as free acetic acid, but this needs confirmation; it is more probable that, as in the stinging hairs of the nettle, it is an unorganized enzyme.

Regarding the structure of the leaf, it may be pointed out that the **stomata** have no special subsidiary cells, but are surrounded by a varied number of ordinary epidermal cells (*Blumenbachia*, *Cajophora*, *Eucnide*, *Mentzelia*, *Petalonyx*). In leaves with bifacial structure (*Cajophora lateritia*, *Eucnide lobata*) the

stomata are found only on the lower side, but they occur on both sides in the centric leaf of *Petalonyx Thurberi*. The leaf-structure in the species last mentioned is specially noteworthy in two other respects, viz. (1) special lignified and pitted cells (water reservoirs ?) adjoin the xylem above and the sclerenchymatous sheath below, in the vascular bundle of the midrib; and (2) a network of tracheides running free in the mesophyll is also present. I have observed oxalate of lime in the leaf of *Mentzelia albescens* only, where it takes the form of clustered crystals, while the crystal-containing cells form groups in the mesophyll. According to Greinert, moreover, it is quite general in this Order for **oxalate of lime** to be present in the form of clustered crystals only.

The **vascular bundles** of the Loaseae, unlike those of the Cucurbitaceae, have simple collateral structure. The herbaceous species, according to Gilg, are like other herbaceous plants in their stem-structure. The mechanical tissue is represented by a strongly developed ring of collenchyma, which shows frequent interruptions At the points of interruption the thin-walled chlorophyll-containing tissue of the stem extends outwards as far as the epidermis, which bears stomata in these regions only. In the woody species a cylinder of wood is present, which in the species investigated by me (*Mentzelia pumila*, Torr. et Gray var. and *Petalonyx Thurberi*, Gray) includes narrow medullary rays, fairly wide vessels with simple perforations and bordered pitting in contact with parenchyma, as well as wood-prosenchyma with fairly wide lumina. In *Petalonyx* these prosenchymatous elements bear exclusively bordered pits, in *Mentzelia* bordered or simple pits. At the outer limit of the bast, which contains some clustered crystals, a few wide-lumened bast-fibres are present in *Mentzelia*, while in *Petalonyx* there are groups of sclerenchymatous parenchyma with yellow walls and cells considerably elongated in the vertical direction. The development of the cork has been observed only in *Mentzelia*, where it takes place immediately on the inner side of the bast-fibres of the pericycle.

Literature: Martinet, Org. de sécrétion, Ann. sc. nat., sér. 5, t. xiv, 1872, p. 183 and pl. 18. —De Bary, Vergl. Anat., 1877, pp. 63, 64.—H. Schenck, Wandverdick. an Pfl.-Haaren, Diss., Bonn, 1884, pp. 12, 13.—Greinert, Morph. u. anat. Verh. d. L. etc., Diss., Freiburg i. Br., 1886, with plate. —Haberlandt, Brennhaare, Sitz.-Ber. Wiener Akad., Bd. xciii, Abt. 1, 1886, p. 123 et seq. and Tab.—[Tassi, Strutt. dei pili di alc. sp. di *Loasa* etc., Siena, 1886.]—Kohl, Kalks. u. Kiesels., Marburg, 1889, pp. 132, 133 and Tab. iv.—Gilg, in Natürl. Pflanzenfam., iii. Teil, Abt. 6a, 1894, p. 101.

TURNERACEAE.

An exhaustive investigation of the anatomical features of this Order has not yet been carried out.

In the structure of the leaf, the chief systematic value attaches to the very varied **hairy covering**, which has been investigated by Urban. This author distinguishes the following forms: (1) simple unicellular hairs (*Turnera sidoides*, L., &c.); (2) stellate hairs: more or less numerous unicellular hairs arise from a small knob or cushion, the central hair being sometimes strongly elongated (*T. Blanchetiana*, Urb., *T. Cearensis*, Urb., *T. hermannioides*, Camb., *T. lamiifolia*, Camb., and almost all species of *Piriqueta* belonging to the section *Eupiriqueta*); (3) uniseriate articulated hairs (*Wormskioldia*, *Streptopetalum* and *Piriqueta Berneriana*, Urb.); (4) capitate hairs: spherical unicellular or indistinctly multicellular structures, which are pellucid and have a very short multicellular stalk (*T. chamaedryfolia*, Camb.); (5) secretory bristles, standing erect and composed of a varying number of rows of cells (but without a vascular bundle), and thicker at the base than at the apex (*Wormskioldia*, *Streptopetalum*, Fig. 83, *A*, *Piriqueta* section *Eupiriqueta*), the

enlargement being either gradual or sudden, the hair sometimes assuming a tuberous form (species of *Wormskioldia*); (6) multicellular yellowish or yellowish-white papillae, ·06–·1 mm. in diameter, resembling the fruit of a *Rubus* in shape, owing to the outer cells projecting convexly: this type is only found in *Turnera* (*T. annularis*, Urb., Fig. 83, *B*, *T. aphrodisiaca*, Ward, *T. calyptrocarpa*, Urb., *T. diffusa*, Willd., *T. hebepetala*, Urb., *T. incana*, Camb., *T. longiflora*, Camb., *T. melochioides*, Camb., *T. odorata*, Rich., *T. opifera*, Mart., *T. stachydifolia*, Urb. et Rolfe).

Regarding the detailed anatomical structure of the forms of trichome mentioned under Nos. 1, 4, 5, and 6, the following statements, based on my own observations, may be added. Judging by what is known to occur in *Turnera annularis*, Urb. and *T. chamaedryfolia*, Camb., the simple unicellular trichomes (1) appear to be characterized by the fact that their basal portion, which is sunk in the epidermis, is narrower than the free body of the hair; in both species also the cells adjoining the hair are somewhat elevated around the latter, so as to form a pedestal. The capitate hairs of *T. chamaedryfolia* (4) have a short or (on the veins of the leaf) a relatively long multiseriate stalk, composed of cells which are longer in the lower and shorter in the upper portion; they also have an approximately spherical multicellular head. The shaggy hairs mentioned under 5 are structures which in *Streptopetalum Hildebrandtii*, Urb. (Fig. 83, *A*) are broad below but become narrower above; thus the lower portion consists of a multiseriate mass of approximately isodiametric cells, whilst in the upper part the rows of cells decrease in number and the cells increase in length, so that the end of the hair is composed of a few long cells forming a single row, the terminal cell being slightly swollen at its tip; in these hairs the secretion is formed in a subcuticular position. Lastly (6) the glands of *Turnera annularis* (Fig. 83, *B*), &c., are sessile, almost spherical, glandular bodies, having a small surface of attachment to the epidermis, and consisting of only one layer of cells, which are radially arranged around the point of attachment; as far as can be determined from herbarium-material, the secretion is subcuticular, as in the bladder-like integumental glands of the Labiatae; the portions of cuticle belonging to the individual glandular cells project convexly outwards, thus giving the gland an appearance similar to that of a fruit of *Rubus*.

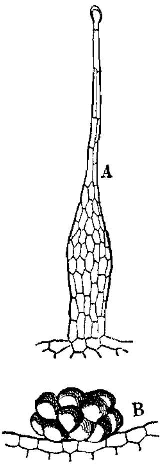

FIG. 83. A, Glandular shaggy hair of *Streptopetalum Hildebrandtii*, Urb. B, Glands of *Turnera annularis*, Urb.—Original.

With the glandular hairs, described above, we may also class the large nectarial glands present on the leaf-base or on the margin of the leaf in certain species of *Turnera*, *Wormskioldia*, *Piriqueta*, and *Mathurina*; they have been investigated in detail by Poulsen in *Turnera*. The stalk of these glands is traversed by a vascular bundle, spreading out in the shape of a fan within the head, which is composed of polygonal cells with thin walls; the secreting surface consists of one layer of prismatic cells, some of which are transversely divided.

The **stomata** are either accompanied by subsidiary cells placed parallel to the pore (*Turnera diffusa*, Willd., according to Gilg; *T. ulmifolia*, L., and *Streptopetalum serratum*, Hochst., according to my own observations), or are surrounded by numerous epidermal cells showing no definite arrangement (*Piriqueta madagascariensis*, Urb.). Gelatinization of the **epidermis** of the leaf appears to occur frequently (*Piriqueta madagascariensis*, *Streptopetalum serratum*, and *Turnera ulmifolia*). **Oxalate of lime**, wherever I have met with it, is excreted in the

form of clustered crystals. Typical internal **secretory elements** are absent. In *Piriqueta madagascariensis* the leaf is speckled with transparent spots owing to the presence in both the upper and lower epidermis of groups of cells which are free from the tannin contained in the remaining epidermal cells; in *Turnera acuta*, Willd., the reverse is the case: tannin is present only in isolated groups of epidermal cells, and the leaf is consequently speckled with dark brown spots (Radlkofer).

The following points may be mentioned regarding the structure of the **wood**. The vessels on the whole do not have very wide lumina (maximum diameter = ·036 mm. in *Piriqueta madagascariensis*, Urb. and ·06 mm. in *Turnera opifera*, Mart.); they are, for the most part, scattered irregularly through the wood and rarely lie in radial series. The perforations are usually simple, but in *Piriqueta* and *Turnera* scalariform perforations with few bars have been observed in the primary wood. In *Piriqueta* and *Turnera* the vessel-wall, where it is in contact with parenchyma, bears bordered pits. The medullary rays are mostly narrow, rarely as much as four cells in breadth. The wood-parenchyma is little developed. In *Turnera diffusa*, Willd., *T. odorata*, Rich., and *T. opifera*, Mart., the wood-prosenchyma, according to Harms, is provided with distinctly bordered pits of varying size (for the most part large); in *Piriqueta aurea*, Urb., the pits are generally small but distinctly bordered; in *Wormskioldia glandulifera*, Klotzsch, the wood-prosenchyma is septate. From the above statements and from those in the work by Turner and in my 'Holzstruktur' it appears that exclusive and typical bordered pitting of the wood-prosenchyma is not shown by all the Turneraceae.

With regard to the structure of the **cortex**, Harms mentions the occurrence of isolated groups of hard bast in the pericycle. In both the species examined by me (*Piriqueta madagascariensis* and *Turnera opifera*) the pericycle is of the same nature. The development of the cork takes place subepidermally in *Turnera opifera*; in the two species mentioned above the cork consists of fairly low thick-walled cells, the inner tangential walls of which are more strongly thickened in *Piriqueta madagascariensis*. The cortex, and chiefly the primary cortex, contains tanniniferous cells, which, especially in *Piriqueta madagascariensis*, appear as idioblasts. In this species the leaf-traces run for a certain distance in the primary cortex as cortical vascular bundles.

Literature: Poulsen, Nectarier, Vidensk. Meddel. naturh. For. Kjöbenhavn, 1881.—Urban, Monogr. d. T., Jahrb. d. bot. Gart. u. bot. Mus. Berlin, Bd. ii, 1883, p. 7.—Turner, Vergl. Anat. der T., Bixaceen etc., Diss., Göttingen, 1885, pp. 58–63.—Solereder, Holzstr., 1885, pp. 138, 139.—Radlkofer, in Sitz.-Ber. Münch. Akad. 1886, p. 318.—Harms, in Engler, Bot. Jahrb., Bd. xv, 1893, pp. 628, 629.—Gilg, in Natürl. Pflanzenfam., iii. Teil, Abt. 6 a, 1893, pp. 58 and 64, Fig. 23.

PASSIFLORACEAE[1].

1. Review of the Anatomical Features. There is an absence of anatomical characters distinctive of the Order and common to all its members. The wood consists of: (1) vessels of varying width, with perforations which are either simple throughout or scalariform with few bars, the latter form being usually confined to the neighbourhood of the primary wood; in *Soyauxia* only are they scalariform throughout; (2) wood-prosenchyma, which bears either bordered or simple pits, and in the latter case is occasionally septate; (3) a little wood-parenchyma and (4) medullary rays of varied breadth. The formation of cork is mostly superficial. The outer limit of the bast is

[1] In the following description the Papayaceae are excluded and are treated separately at the end of the Passifloraceae.

formed by a composite and continuous sclerenchymatous ring or by isolated groups of bast-fibres. It is characteristic of the mature leaves that no special type in the arrangement of the neighbouring cells around the guard-cells can be detected. The hairy covering is formed by simple unicellular or uniseriate hairs, by unicellular hairs curved in the form of a hook (in species of *Passiflora*), and by glandular shaggy hairs with stalks of varying length (species of *Passiflora*, Fig. 84, *B*, and *Malesherbia*); glandular spots on the leaf are found in species of *Adenia* and *Passiflora*; large nectarial glands occur on the petiole in many species. Intercellular secretory receptacles with brown contents are present in the leaf of species of *Ophiocaulon*, elongated tannin-sacs in the branches of species of the genera *Passiflora*, *Hollrungia*, and *Ophiocaulon*. Oxalate of lime is excreted in the form of ordinary solitary and clustered crystals. A series of anatomical features of the leaf, such as a two-layered epidermis (*Adenia*, *Hollrungia*, *Smeathmannia*), a mucilaginous epidermis (*Barteria*, *Paropsia*), papillose differentiation of the lower epidermis (*Adenia*, *Echinothamnus*, *Ophiocaulon*), cuticular protuberances (*Passiflora*), spicular cells in the mesophyll (*Passiflora*), crystal-idioblasts and enlarged mesophyll-cells with brown contents, are of value for specific diagnosis.

2. STRUCTURE OF THE LEAF [1]. The leaves of most of the Passifloraceae are bifacial in structure. The following species have centric or almost centric structure: *Tryphostemma nummularium*, Engl., *Echinothamnus Pechuëlii*, Engl., *Adenia glauca*, Schinz., *A. repanda*, Engl., *Passiflora Mooreana*, Hook., *Paropsia grewioides*, Welw., and *P. reticulata*, Engl., as well as the two genera *Malesherbia* and *Gynopleura* of the Malesherbieae. The mesophyll shows only a few special features. The middle layers of the spongy tissue of *Mitostemma Glaziovii*, Mart., contain thickened and pitted cells; in *Passiflora arborea*, Spreng., and in a plant probably identical with *P. citrifolia*, Mast., numerous spicular cells, with an irregular course, are stated by Harms to occur in the mesophyll.

The **epidermal cells** have straight or undulated lateral walls. According to Harms, a 'two-layered epidermis' (the lower layer containing numerous solitary and clustered crystals) occurs on the upper side of the leaf in *Hollrungia aurantioides*, K. Schum., *Smeathmannia pubescens*, R. Br., and *Barteria fistulosa*, Mast. [2], while an epidermis consisting almost throughout of two layers is found in *Adenia populifolia*, Engl. In *Paropsia obscura*, Hoffm. [3], and *Barteria fistulosa*, according to my own observations, the epidermis on the upper side of the leaf includes cells with mucilaginous inner membranes. According to Harms, papillose differentiation of the lower epidermis is widely distributed in the genera *Adenia*, *Ophiocaulon*, and *Echinothamnus*. Finally, the epidermis of the leaf and stem in many species of *Passiflora* belonging to the sections *Cieca*, *Decaloba*, and *Eumurucuya* is characterized by cuticular protuberances, whilst in other sections these structures are only of isolated occurrence, e. g. within the subgenus *Astrophea* in *Passiflora spinosa*, Mast.

The **stomata** usually occur only on the lower side of the leaf; they are present on both sides of the leaf in *Keramanthus Kirkii*, Hook. fil., and in the

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[1] The most important work is: Harms, loc. cit. He investigated the following genera: I. Malesherbieae: *Malesherbia*, *Gynopleura*; II. Passifloreae: *Passiflora*, *Tacsonia*, *Mitostemma*, *Tryphostemma*, *Paropsia*, *Paropsiopsis*, *Smeathmannia*, *Barteria*, *Hollrungia*; III. Modecceae: *Modecca* (*Adenia*), *Echinothamnus*, *Keramanthus*, *Ophiocaulon*; IV. Acharieae: *Acharia*, *Ceratiosicyos*; genera anomala: *Physena*, *Soyauxia*. Withr ieference to this we may remark that the genera *Paropsia*, *Paropsiopsis*, *Smeathmannia*, and *Barteria* are separated by Harms as the group Paropsieae, while he unites the rest of the Passifloraceae with the Modecceae to constitute the Passifloreae.

[2] In a specimen of *Barteria fistulosa* sent to me from Berlin I find only a one-layered epidermis, which, however, includes mucilaginous cells.

[3] Harms interpreted the mucilaginous cells of *Paropsia obscura* incorrectly; possibly this may to some extent also apply to the two-layered epidermis of *Smeathmannia pubescens*, &c.

Malesherbieae. In the mature leaf no specially characteristic arrangement of the neighbouring cells around the guard-cells can be recognized.

The systems of vascular bundles in the smaller veins, so far as is known, are embedded. They may or may not be accompanied by sclerenchyma, which, according to Harms, is usually absent in the members of his Passifloreae, as also in *Acharia* and *Ceratiosicyos*, while the Paropsieae of Harms contain sclerenchyma in the veins. In *Soyauxia gabonensis*, Oliv. and *Physena madagascariensis*, Steud. the bundle-system is enclosed by a ring of sclerenchyma.

Oxalate of lime is present in the tissue of the leaf and axis in the form of rhombohedra and of clustered crystals. Special crystal-sacs are stated by Harms to occur in the mesophyll of certain species of *Adenia*, *Ophiocaulon*, and *Soyauxia*. In *Adenia* they usually (*A. australis*, Engl., *A. cardiophylla*, Engl., *A. panduraeformis*, Engl., *A. populifolia*, Engl., *A. Schweinfurthi*, Engl., *A. trilobata*, Engl., *A. Wightiana*, Engl.) contain solitary, rarely (*A. repanda*, Engl.) clustered crystals. In *Adenia* the solitary crystals are as a rule enclosed in a cellulose-sheath, which is in connexion with the longitudinal walls of the crystal-cells. In *A. lanceolata*, Engl. and *A. Welwitschii*, Engl. the entire mesophyll is filled with clustered crystals. Crystal-idioblasts, identical with those of *Adenia*, are also met with in *Ophiocaulon lanceolatum*, Engl. and *O. Poggei*, Engl., while the crystal-cells of *Soyauxia gabonensis*, Oliv. contain

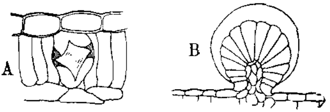

FIG. 84. A, Crystal-cell from the palisade-tissue of *Adenia obata*, Engl. B, Glandular shaggy hair of *Passiflora clathrata*, Mast. in longitudinal section.—A Original, B after Harms.

clustered crystals, which are embedded in a thickening of the wall of the (usually spherical) idioblasts; the thickening lies on that wall which is directed towards the interior of the leaf. In connexion with the crystals we may mention the fact that Zimmermann has observed spindle-shaped bodies in the mesophyll-cells of *Passiflora caerulea*; these bodies are situated in the cell-sap, and are probably of the nature of crystalloids. In the epidermis of the leaf of *Passiflora rotundifolia*, L. and *P. ichthyura*, Mast., sphaero-crystalline masses of unknown nature occur, according to Harms.

Among internal **secretory organs** the most noteworthy are the intercellular, spherical and apparently schizogenous secretory receptacles in the interior of the leaf in the species of *Ophiocaulon* (*O. cissampeloides*, Mast., *O. gummiferum*, Mast., *O. Poggei*, Engl. and *O. lanceolatum*, Engl.); they are filled with blackish-brown tanniniferous contents, and give rise to a black dotting of the leaf. Cells filled with the same brown, tanniniferous contents, and usually distinguished from the neighbouring cells by larger lumina, are found in the palisade-tissue of the three first-named species of *Ophiocaulon*, and in the spongy tissue of *O. lanceolatum*, Engl. and *Adenia Schweinfurthi*, Engl. The axis resembles the leaf in containing tanniniferous cells, which in certain Passifloraceae are developed as tannin-sacs; these mostly have wide lumina, often have thick walls and are frequently considerably elongated in the vertical direction: e.g. according to Harms in the pith and cortex of *Passiflora holosericea*, L. in the pith of *Hollrungia aurantioides*, K. Schum., and lastly in the pith of *Ophiocaulon Poggei*, Engl., where they are spindle-shaped and sclerenchymatous.

The **hairy covering** is formed by unicellular or uniseriate clothing hairs, and by glandular shaggy hairs. In the species of *Passiflora* both forms of clothing hair occur, with walls of varying thickness; accompanying these hairs in certain species (*P. acerifolia*, Cham. et Schlecht., *P. bryonioides*, H.B.K., *P. inamoena*, A. Gray, *P. sicyoides*, Cham. et Schlecht.) there are unicellular trichomes, which are curved in the form of a hook at the apex. In *Acharia tragioides*, Thunb. ordinary uniseriate hairs have been observed, in *Paropsia* ordinary unicellular hairs, while in many species of *Tacsonia* there are very long uniseriate hairs, which are occasionally (*T. lanata*, Juss.) interwoven like felt; lastly, in the Malesherbieae stiff unicellular trichomes are found. Glandular shaggy hairs (Fig. 84, *B*) are found only in *Passiflora* and *Malesherbia*. In the genus *Passiflora*, in which they are restricted to certain species of the section *Dysosmia* (*P. clathrata*, Mast., *P. foetida*, L., *P. lepidota*, Mast., *P. villosa*, Vell.), the glandular shaggy hairs have a multiseriate stalk, which is of variable length and, when long, sometimes contains a vascular bundle. The glandular head itself consists of a multiseriate core of elongated cells, which, as it were, forms the continuation of the stalk, and of a secretory palisade-like epidermis. The glandular shaggy hairs of *Malesherbia* have a different type of structure; they are long, filiform, multiseriate bodies, which are pointed or (*M. thyrsiflora*, R. et P.) rounded off at the apex; their secretion produces the well-known disagreeable smell of the Malesherbieae. In addition to the glandular shaggy hairs, glandular spots are met with on the lower side of the leaf in some members of the Order, namely in the genus *Passiflora* and in *Adenia cardiophylla*, Engl. Within the genus *Passiflora* these spots are restricted to species of the sections *Cieca*, *Decaloba*, and *Eumurucuya*, whilst in other sections they are either absent (*Astrophea*, *Psilanthus*) or only occur in relatively small numbers (*P. pulchella*, H.B.K. belonging to the subgenus *Grenadilla*). Externally these glandular spots appear as round brown specks on the lower side of the leaf. According to Harms, their structure is as follows in *P. rotundifolia*, L. In a superficial section radially elongated epidermal cells are to be observed at the periphery of the glandular spot; nearer the centre these are adjoined by cells, the walls of which become more and more thickened and their lumina narrower, so that the actual glandular spot is enclosed by a rampart of thick-walled cells. These cells then pass over into the secretory tissue, the cells of which have a polygonal outline in surface-view, but are seen to be moderately elongated in a transverse section of the leaf. Several layers of these prismatic cells lie one above another; finally, towards the interior of the leaf, they merge into a small-celled tissue filled with clustered crystals (compare also Morini). The large sessile or shortly stalked glands, which occur so frequently on the petioles in this Order (in *Passiflora*, *Tacsonia*, *Deidamia*, *Smeathmannia*, *Crossostemma*, *Modecca*, and *Ophiocaulon*, according to Bentham and Hooker), are merely a modification of these glandular spots. In *P. brasiliana*, according to Martinet, they possess a glandular epithelium similar to that of the glandular spots, and the multiseriate stalk contains a vascular bundle.

3. Structure of the Axis[1]. The axis, even in the climbing forms, has normal structure[2].

The epidermis in the young shoots of several species of *Adenia*, *Ophiocaulon* (especially *O. gummiferum*, Mast.), and *Echinothamnus* possesses a deposit of an incrusting wax-like substance. The formation of **cork** usually takes place superficially, in the epidermis or in the subepidermal layer of

[1] Most important literature: Solereder and Harms, ll. cc.

[2] The correctness of the statement (made by Schwendener, Mech. Prinz., 1874, p. 150) as to the occurrence of medullary vascular bundles in *Passiflora trifasciata* is doubtful.

cells. Transformation of the outermost layer of cortical cells into the cork-cambium is stated by Harms to occur in *Passiflora*, the Paropsieae and *Soyauxia*. In *Acharia tragioides*, which is characterized by the five-angled cross-section of the stem, the formation of phellogen begins immediately on the inner side of the strands of collenchyma, which occupy the angles, and is continued subepidermally in the parts of the stem situated between the angles. In *Malesherbia* the cork arises either in the epidermis itself (*M. pulchra*, Ph.), or subepidermally (*M. densiflora*, Ph.), or in a cell-layer situated at a depth of 8–10 layers below the epidermis (*M. thyrsiflora*, R. et P.). The cork-cells are in all cases described as having thin walls. The spongy cork of *Passiflora suberosa* specially deserves mention; it consists of cells, which are strongly elongated radially, and, according to Höhnel, are not suberized. The primary **cortex** frequently contains collenchymatous tissue; in *Malesherbia fasciculata*, Don, a many-layered palisade-tissue is developed below the epidermis. The pericycle includes isolated groups of bast-fibres or a sclerenchymatous ring. Isolated groups of bast-fibres occur in species of *Passiflora*, *Adenia*, *Keramanthus*, in *Acharia* and *Ceratiosicyos*, in *Paropsia obscura*, Hoffm. and *Barteria Braunii*, Engl., as well as in *Gynopleura* and *Malesherbia*; a composite and continuous sclerenchymatous ring is found in *Mitostemma Glaziovii*, Mast., in the older branches of *Barteria Braunii*, in *Smeathmannia laevigata*, R. Br., *S. pubescens*, R. Br., *Paropsiopsis africana*, Engl., and *Soyauxia*; a sclerenchymatous ring composed solely of short or elongated parenchyma-shaped sclerenchymatous cells is present in *Physena*. Secondary hard bast occurs (species of *Passiflora*; *Soyauxia*). The structure of the wall of the bast-fibres in many species of *Passiflora* (especially in those belonging to the sections *Cieca*, *Decaloba* and *Eumurucuya*, but also in *P. acerifolia* Cham. et Schlecht., and *P. pulchella*, H.B.K.), which is distinctly seen on treating a transverse section with chlor-zinc-iodine, may also be mentioned; the strongly thickened walls of the bast-fibres become violet, while the network of middle-lamellae is stained yellowish (Sanio, Harms).

The following points may be mentioned in the structure of the **wood**. The breadth of the medullary rays varies. Broad medullary rays occur both in climbing species and in those which do not climb (*Passiflora arborea*, Spruce, *P. caerulea*, L., *Keramanthus Kirkii*, Hook. f., *Echinothamnus Pechuelii*, Engl., *Adenia globosa*, Engl., *Tryphostemma littorale*, Engl., *Ceratiosicyos Eckloni*, Nees). In other species the medullary rays are not more than four cells in breadth. As regards the shape of the cells of the medullary rays a remarkable feature is that in *Tryphostemma littorale*, *Echinothamnus Pechuelii* and *Ophiocaulon Poggei*, Engl. they are often elongated more in the tangential than in the radial direction. The size of the lumina of the vessels likewise varies greatly in this Order. In the genus *Passiflora*, which climbs by means of tendrils, especially in *P. spicata*, Mart., the diameter of the vessels attains ·22 mm., while in *Acharia tragioides* (fruticulus!) it only reaches ·024 mm. The perforations of the vessels are usually simple; in certain Passifloraceae, however, accompanying the simple perforations, others of the scalariform type, with a variable number of bars, are present in different proportions; the anomalous genus *Soyauxia* alone possesses exclusively scalariform perforations.

The following special details regarding the manner of perforation of the vessels are derived from Harms' work. The Passifloreae of Harms have simple perforations only, with the exception of *Mitostemma Glaziovii*, Mast., in which scalariform perforations also occur. The vessels of *Ceratiosicyos Ecklоni*, which are provided with very wide lumina, have simple perforations only, while in *Acharia tragioides*, scalariform perforations with one or two bars have been observed in the neighbourhood of the primary wood. The Paropsieae of Harms are in general characterized by the joint occurrence of both forms of perforation (the scalariform type having 1–20 bars);

only in *Paropsia reticulata*, Engl. are simple perforations stated to occur throughout. In the Malesherbieae, simple perforations predominate, scalariform perforations with 1–3 bars being also present, especially in the neighbourhood of the primary wood. *Physena*, again, possesses only simple perforations.

The structure of the wall of the vessel, where it is in contact with the parenchyma of the medullary rays, varies. At these places fairly large rounded pits are stated to occur in *Mitostemma Glaziovii*, Mast. and *Passiflora arborea*, Spreng.; in *Adenia venenata*, Forsk. and *Keramanthus Kirkii*, Hook. fil. all transitions from simple to bordered pits are found; in *Hollrungia aurantioides*, K. Schum. chiefly bordered pits; in *Passiflora Vespertilio*, L., *Adenia trilobata*, Engl., in the Malesherbieae and in *Soyauxia* bordered pits only. Wood-parenchyma is for the most part scantily developed, but is fairly abundant in *Soyauxia*. The wood-prosenchyma may have either distinctly bordered or simple pits; among the simple pits I include those cases in which the pits are provided with a small and often indistinct border. The wood-prosenchyma with simple pits is occasionally (*Acharia, Ceratiosicyos, Gynopleura*) septate by means of delicate division-walls.

Wood-prosenchyma with bordered pits occurs in: *Passiflora*, *Tacsonia*, *Hollrungia aurantioides*, K. Schum., *Tryphostemma niloticum*, Engl., *T. littorale*, Engl., *T. Hanningtonianum*, Mast., *Adenia lanceolata*, Engl., *A. trilobata*, Engl., *Ophiocaulon gummiferum*, Mast., and *Soyauxia*; on the other hand, wood-prosenchyma with simple pits is found in: *Keramanthus Kirkii*, Hook. fil., *Echinothamnus Pechuelii*, Engl., *Adenia aculeata*, Engl., *A. globosa*, Engl., *A. venenata*, Forsk., *Acharia*, *Ceratiosicyos*, the Paropsieae and Malesherbieae.

Literature: Sanio, in Bot. Zeit. 1860, p. 209 et seq.—Martinet, Org. de sécrétion, Ann. sc. nat., sér. 5, t. xiv, 1872, pp. 191, 192 and pl. 19.—Reinke, in Pringsheim Jahrb., Bd. x, 1876, p. 168, 169.—De Bary, Vergl. Anat., 1877.—Solereder, Holzstr., 1885, p. 139.—Turner, Vergl. Anat. d. Bixaceae etc., Diss., Gottingen, 1885.—Morini, Nett. estranuz., Mem. Accad. Bologna 1886, p. 349 and Tab. ii, iii.—Zimmermann, Pflanzenzelle, 2. Heft, 1891, p. 157.—Harms, Verw. d. anat. Baues für die Umgr. u. Einteil. d. P., Engler, Bot. Jahrb., Bd. xv, 1893, p. 548 to 633 and Tab. xxi.—H. Schenck, Anat. d. Lianen, 1893, p. 148.—Harms, in Natürl. Pflanzenfam., iii. Teil, Abt. 6 a, 1893, pp. 66 and 71

PAPAYACEAE.

The Papayaceae[1], which must certainly be separated from the Passifloraceae, are especially characterized by the possession of articulated **laticiferous tubes**, which occur in all parts of the plant. In the axis of *Carica* they occur in the pith, wood and cortex, and in the same position in the root; in the latter the laticiferous tubes situated on the inner side of the endodermis are in connexion with those on the outer side. In the leaf of *Carica* and *Jacaratia* laticiferous tubes are principally to be found accompanying the vascular bundles; they are, however, frequently prolonged for a certain distance beyond the ends of the vascular bundles and penetrate into the mesophyll, in *Carica Papaya* even as far as the epidermis. The laticiferous tubes of the Papayaceae, as Rüger has shown in the case of *Carica*, do not form a dead framework of cells filled with secretion, but remain permanently in the condition of living cells, owing to the presence of a protoplasmic lining and of well-differentiated nuclei. The secretion itself is finely granular and is stained yellow by iodine-solution. As is well known, it contains a ferment—papaïn—which peptonizes proteids (Wittmack, Wurtz, Bouchut, &c.). We may add that Guignard has recently discovered a second ferment in the Papayaceae, identical with myrosin, and a glucoside, agreeing with myronate of potash. Contrary to the case of the Cruciferae (q.v.), the myrosin

[1] *Carica* is the only genus which has been investigated in detail.

in the Papayaceae is not localized in special cells. The cells observed in the latter Order which are distinguished by their shape, and are filled with special contents, have nothing to do with myrosin-cells, but some of them are tanniniferous, while others are laticiferous cells; the latter occur in relation to the laticiferous tubes.

In transverse section the **axis** of *Carica* shows a ring of vascular bundles, which are separated from one another by broad, radially placed strips of parenchyma, corresponding to medullary rays. The vascular bundles become further divided up by similarly constituted secondary medullary rays. The xylem-mass consists of unlignified tissue, in which the vessels are embedded; the vessels bear simple pits, are thickened in a reticulate or scalariform manner, and have simple perforations. Wood-prosenchyma is wanting. The pericycle contains isolated groups of hard bast. The secondary phloem is stratified into hard and soft zones. The primary cortex is in part differentiated as collenchyma. The swelling, which is apparent at the base of the stem of *Carica*, is due to dilatation of the primary cortical tissue and of the pith.

In *Carica Papaya* the **leaf** is bifacial in structure; the spongy tissue is lacunar. In this species and also in *Jacaratia Solmsii*, Urb., the stomata occur only on the lower side of the leaf, and are surrounded by several ordinary epidermal cells. In the leaf, oxalate of lime is excreted in the form of clustered crystals.

Finally it may be mentioned that, in the parenchymatous tissues of all parts of the plant, Rüger has observed peculiar, strongly refractive grains of rather large size and of rounded or irregular shape; these, in view of their chemical reactions, are supposed to consist of a substance of the nature of an aldehyde.

Literature: Schacht, in Monatsber. Berliner Akad., 13. Nov. 1856, pp. 515–534 and 2 Tab.—Hanstein, Milchsaftgef., 1864, p. 61 et seq.—Dippel, Entsteh. d. Milchsaftgef., Rotterdam, 1865.—De Bary, Vergl. Anat., 1877.—Wittmack, in Bot. Zeitung 1878, p. 532 et seq.—E. Schmidt, Plasmak. d. gegl. Milchr., Bot. Zeit. 1882, pp. 451–4.—Solereder, Holzstr., 1885, p. 139.—Pirotta e Marcatili, Ancora sui rapporti tra i vasi laticiferi ecc., Ann. R. Ist. bot. di Roma, Anno ii, 1886, n. 2; abstr. in Just 1886, i, p. 922.—Rüger, Beitr. z. Kenntn. d. Gatt. *Carica*, Diss., Erlangen, 1887.—Groom, Funct. of laticif. tubes, Annals of bot., vol. iii, 1889, pp. 164, 165.—Guignard, Princ. actifs chez les P., Journ. de bot., t. viii, 1894, pp. 67 and 85 et seq.—Solms-Laubach, in Natürl. Pflanzenfam., iii. Teil, Abt. 6 a, 1894, p. 97.

CUCURBITACEAE.

1. Review of the Anatomical Features. This Order is well characterized anatomically. In almost all Cucurbitaceae the vascular bundles are bicollateral in structure; the only exception to this is afforded by members of the tribes Gynostemmeae, Zanonieae, and Feuilleae. The vascular bundles are always separated from one another by broad strips of ground-tissue. In the herbaceous species a sclerenchymatous ring, which is usually continuous, is developed in the cortex; in these forms the vascular bundles are also as a rule arranged in two rings, but these may be referred to a single ring in which the alternate bundles project more strongly. In the species with secondary thickening broad secondary medullary rays arise in the vascular bundles, dividing the latter dichotomously, and in these plants the external strengthening ring is reduced to isolated groups of sclerenchyma-fibres. The wood-vessels, which as a rule have very wide lumina, possess simple perforations. The occurrence of sieve-tubes in the stem outside the fibro-vascular system is a wide-spread phenomenon. A definite type of stoma does not appear in the Order. Oxalate of lime has hitherto been rarely observed, and only in the form of solitary crystals. Internal secretory receptacles are wanting.

The hairy covering consists of (*a*) simple unicellular or uniseriate hairs, the base of which is sometimes surrounded by subsidiary cells, (*b*) wart-like or spiny trichomes, and (*c*) shortly stalked glandular hairs composed of few cells. A very common feature in the Order is the occurrence of cystolith-like structures, which are found in the cells of the hairs and in the neighbouring cells, whether belonging to the epidermis or the mesophyll; these structures are connected by transitional forms, on the one hand with merely calcified and thickened cell-membranes (see also Fig. 86), and on the other hand with true cystoliths, which (as double cystoliths or larger groups, Fig. 85) have been observed in the genera *Momordica* and *Coccinia* only. Lastly, silicified cell-membranes are not rare in the Order.

Anomalous stem-structure has only been observed in *Wilbrandia verticillata*, Cogn., where the cambium of the inner phloem-bundles produces wood-elements locally. Anomalous root-structure is more frequent; in *Cucurbita* and *Thladiantha* the wood of the root contains phloem-islands; in *Bryonia dioica* concentric vascular bundles arise secondarily in the wood of the root; the root of *Ecballium Elaterium* forms extrafascicular rings of growth.

2. Structure of the Leaf. A comprehensive investigation of the leaf-structure in this Order has not yet been made. My own general preliminary investigations have shown that bifacial as well as centric leaf-structure occurs, and that **stomata** may either be present on both sides of the leaf, or only on the lower surface. No special type of stoma characterizes the Cucurbitaceae. The pair of guard-cells is surrounded without special orientation by an indefinite number of ordinary epidermal cells or by cells distinguished only by their small size [1]. I have not met with a mucilaginous epidermis in any case. In *Feuillea cordifolia*, L. a one-layered **hypoderm** is developed beneath the upper epidermis. **Oxalate of lime** appears to be but rarely present in the Cucurbitaceae. I have not observed it in the leaf in any case, and in the axis in *Zanonia indica*, L. only, where it is deposited within stone-cells, and has the ordinary rhombohedral form. The **hairy covering** of the vegetative organs, as far as is known, consists of (1) simple, unicellular or uniseriate hairs, not uncommonly accompanied by subsidiary cells, which are sometimes raised above the base of the hair like a pedestal; (2) wart-like or spiny trichomes, in the formation of which the periblem is concerned to a varying extent, in addition to the integumental tissue (species of *Bryonia*, *Cucumis*, *Cucurbita*, and *Ecballium*); and (3) glandular hairs. The glandular hairs, which I have seen on the leaf in *Feuillea cordifolia*, L., *Zanonia indica*, L., *Abobra tenuifolia*, Cogn., *Cyclanthera explodens*, Naud., and *Gynostemma integrifolia*, Cogn., consist of a fairly short uniseriate, few-celled stalk and a spherical or ellipsoid, glandular head composed of a small number of cells. Similar capitate hairs have been met with by Uhlworm in *Cucurbita Pepo* and *Ecballium agreste*, and by Volkens in *Citrullus Colocynthis*, Schrad. Martinet has figured glandular hairs with a longer uniseriate stalk and a disc-shaped head, divided by vertical walls into four cells, in *Cucumis Melo*. We may also mention that the leaf-teeth of the young leaves occasionally produce a mucilaginous secretion; e.g. according to Reinke in *Cucumis Melo*, where the tips of the leaves consist of a thin-walled parenchyma, filled with dense contents, and are clothed with a small-celled epidermis, which includes a few stomata on the upper side of the leaf above the termination of the vein [2].

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[1] The much-elevated stomata on high pedestals found on the fruit-stalk of *Cucurbita Pepo* may be mentioned here, because they possibly occur on the leaves also [cf. Fig. 169 in Haberlandt's Physiolog. Pflanzenanatomie, ii Aufl.).

[2] We may also mention here the vermiform trichomes (consisting of a row of short cells) as well as the branched hairs with a uniseriate axis and a few unicellular branches, observed by Uhlworm

The occurrence of **cystoliths or cystolith-like structures** is very characteristic of many members of the Order. True cystoliths, in the form of double cystoliths, are known only in the genera *Momordica* (Fig. 85, *A–C*) and *Coccinia*. Penzig first observed them in *Momordica Charantia*, L. and in a plant described as *Momordica echinata*, W.; the latter plant, however, according to Radlkofer, certainly does not belong to *M. echinata*, W. = *Echinocystis lobata*, Torr. et

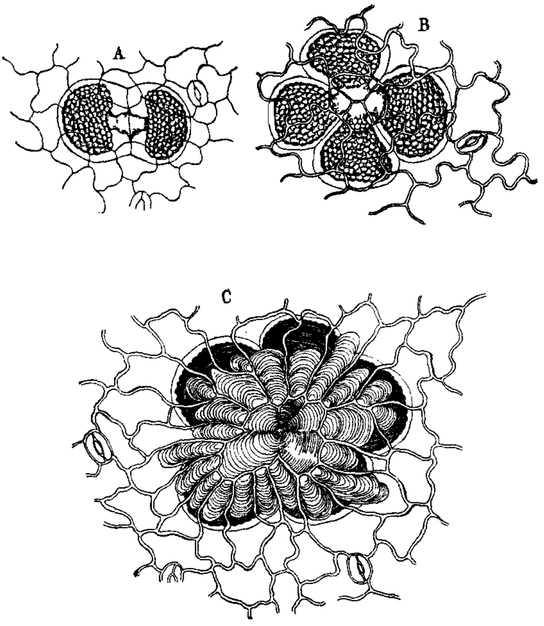

FIG. 85. Double cystoliths and groups of cystoliths in *Momordica*: A, B, *Momordica* sp.; C, *Momordica Charantia*, L.—After Penzig.

Gray, but is another species of *Momordica*; the true cystoliths were subsequently also observed by Radlkofer in *M. pterocarpa*, Hochst. The cystoliths of *Momordica* to which we refer are found in the epidermis on the lower side of the leaf, two or more (3–4) epidermal cells, situated side by side, and extending into the mesophyll to a considerable depth, containing the cysto-

on the petals of *Cucurbita Pepo* and in *Ecballium agreste*; for possibly hairs of this type may occur also on the vegetative organs of these or other members of the Order.

liths. Each cell encloses a cystolith, which is provided with a distinct stalk incrusted with a siliceous substance, while the principal part is strongly calcified, and after decalcification shows neither the reaction of cellulose nor of wood nor of cork. The stalks of the cystoliths are attached at corresponding points to the common wall of contact. In the plant described as *Momordica echinata*, Penzig chiefly met with double cystoliths, more rarely with groups of 3–4 cells (lithocysts) containing them. In *Momordica Charantia* double cystoliths are only rarely present, there being usually groups of 3–4 lithocysts; here cystolith-formation occasionally appears secondarily in the ordinary epidermal cells, adjoining these groups. These secondary cystoliths are smaller, narrowly club-shaped structures, inserted singly and by a broad base on that vertical wall (of the epidermal lithocyst), which is turned towards the group. In *Momordica Charantia*, and still more clearly in *M. pterocarpa*, Radlkofer observed regular sieve-fields on the cells containing the large cystoliths; the sieve-areas clearly facilitate communication between these cells and the neighbouring mesophyll-cells, and are often developed in connexion with a whole ring of these adjacent cells. This fact is in agreement with Fellerer's observation that the common wall between the cystolith-cells of *Momordica* also has a structure resembling that of sieve-fields. The cystoliths of *Coccinia*, which Avetta discovered in *C. palmata*, Cogn., agree essentially with those of *Momordica*. Those groups, which consist of four cystolith-cells, differ from those of *Momordica* in two ways: they are present in the epidermis on the upper side of the leaf, and are as a rule considerably larger. In *Coccinia*, as in *Momordica Charantia*, the formation of cystoliths is continued in the adjacent epidermal cells.

The cystolith-like structures, which are widely distributed in the Cucurbitaceae, are usually restricted to the cells of the hairs and to the neighbouring cells; the latter either belong to the epidermis only, or to the mesophyll also. They are often so much reduced in size that they can no longer be spoken of as cystoliths. Those most resembling cystoliths are protuberances of the cell-wall, variable in shape and without a stalk; they are mostly impregnated with carbonate of lime, and project convexly into the cell-lumen; they are similar to the smaller cystoliths described above as occurring in the cells adjacent to the large cystolith-cells in *Momordica Charantia* and in *Coccinia*. From these structures all transitions to a mere calcified thickening of the wall are found. The hair-cells themselves rarely contain cystolithic protuberances, which are of much more frequent occurrence in the cells adjacent to the hairs, but the hair always appears as the centre of calcification and cystolith-formation, and therefore the points of attachment of the cystolithic protuberances in the subsidiary cells are directed towards it. Very frequently the formation of cystolith-like structures extends to a considerable distance from the hair along the surface of the leaf, so that the groups of cells in which these structures occur become visible to the naked eye as small round white areas—false scales—e.g. in *Bryonia alba* or *Coccinia quinqueloba*, Cogn. It is also noteworthy that in the cystolith-like structures under consideration (as in the cystoliths themselves), silica occurs as an infiltration accompanying the lime and sometimes exceeding the latter in amount, e.g. in the false scales of *Coccinia cordifolia*, Cogn. β *Wightiana* (according to Radlkofer).

The cystolith-like structures have been investigated in detail by Kohl in a relatively large number of Cucurbitaceae (species of the genera *Benincasa*, *Bryonia*, *Coccinia*, *Cucurbita*, *Cucumis*, *Cyclanthera*, *Luffa*, *Momordica*, *Prasopepon*, *Sicyos*, and *Thladiantha*), as well as by Radlkofer. In '*Luffa marylandica*' and *Thladiantha dubia* cystolith-like bodies are completely absent, according to Kohl, and the walls of the hairs are only slightly calcified. *Prasopepon Duriaei* only shows occasional slight thickenings of the membrane in the basal portion of the hair. *Coccinia*

indica, on the other hand, has a more strongly thickened and calcified hair-base; in this plant there also occur groups of ordinary epidermal cells having their common walls strongly thickened and calcified. The white scale-like structures on the upper side of the leaf of *Coccinia Moghadd*, Aschers., are due to groups of epidermal cells, the central cells of which penetrate fairly deep into the mesophyll, whilst the external walls and the common walls of contact are thickened and calcified. *Cyclanthera explodens*, *Sicyos angulatus*, *S. bryoniaefolius*, *Cucumis*, and *Benincasa cylindrica* agree rather closely as regards the formation of cystoliths. In these plants the cells lying around the base of the hair (in part also belonging to the mesophyll) are provided with calcified thickenings of their cell-walls, having the form of pegs in *Sicyos angulatus* and *Benincasa cylindrica*, while they are less prominent in *Cyclanthera explodens* and *Sicyos bryoniaefolius*. In the cells of the short, multicellular, wart-like trichomes on both sides of the leaf in *Bryonia alba* the walls possess thickenings which become calcified; in some cases one can recognize, by the presence of a short stalk, that the thickenings are distinctly of the nature of cystoliths. Radlkofer met with similar more or less distinct cystolith-formations in the cells adjoining the hairs in the species of *Coccinia* and *Momordica* mentioned above; here they give rise to false scales as in *Bryonia*.

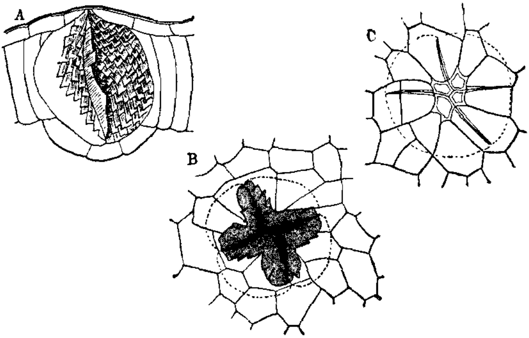

FIG. 86. Deposits of carbonate of lime in the leaf of *Hanburia mexicana*, Seem. A, Incrusted group of cells in a transverse section of the leaf; B, in surface-view (before decalcification; the central epidermal cells lying above the cell-group are not figured); C, in surface-view after decalcification.—Original.

Before leaving the subject of cystolithic formations, we may mention a special case of calcareous incrustation of the cell-wall occurring independently of the hairs, and observed by me in *Hanburia mexicana*, Seem. (Bourgeau, No. 2426, Mexico); it belongs to the same category as the structure found in *Coccinia Moghadd*, and referred to above. This calcareous incrustation (Fig. 86) extends to groups of three to four epidermal cells situated side by side on the upper surface of the leaf. Like the cystolith-cells of *Momordica*, the cells in question are distinguished from the rest of the epidermal cells by their considerable size; only a small portion of each cell is exposed on the surface of the leaf, but they penetrate proportionately deep into the palisade-tissue, together forming an approximately spherical group. The common walls of contact of these cells are only slightly thickened, and are completely covered by an incrustation of rhombohedral crystals of carbonate of lime. In superficial aspect (Fig. 86, *B*) the incrusted cell-walls of each group appear like

a cystolith composed of four or more rays, similar to those which occur in the Gynocarpean genus *Sparattanthelium*. In a dried leaf the cell-groups are visible to the naked eye as granular dots.

Silicification, besides occurring in the cystoliths and cystolith-like formations and in the cells containing them, is also met with in the mesophyll in some members of the Order, as I have observed in *Zanonia indica*, L. and *Feuillea cordifolia*, L. In *Zanonia indica* the silicified cells are arranged in the form of a sphere, and the walls which abut on one another at the centre of the sphere, as well as those which run radially, are more strongly thickened and silicified; more rarely the silicification also extends to ordinary cells of the palisade-tissue. In *Feuillea cordifolia* groups of cells, belonging as a rule to the palisade-tissue, are found to differ from the remaining cells of this tissue in their greater elongation, and in becoming silicified; occasionally the spongy tissue situated below these cells also takes part in the formation of the silicified group.

The **petiole** of the Cucurbitaceae contains isolated vascular bundles in the species investigated by Petit, belonging to the genera *Bryonia*, *Cucumis*, *Cucurbita*, *Cyclanthera*, *Ecballium*, *Lagenaria*, *Luffa*, *Melothria*, and *Sicyos*; these bundles are arranged in the form of a horse-shoe or a circle in transverse section, those of larger size having bicollateral structure. The number of the bundles varies both in the initial and in the characteristic region.

3. STRUCTURE OF THE AXIS. The characteristic features common to the Order, viz. the bicollateral structure of the vascular bundles, to which there are few exceptions, the arrangement of the isolated vascular bundles in two rings (this arrangement, however, becoming subsequently obliterated in the axis of those species which have secondary thickening), the presence of a usually continuous strengthening ring in the cortex and the simple perforations of the vessels, have already been duly emphasized above. We will now refer to these features and some others in greater detail.

The bicollateral nature [1] of the **vascular bundles** in this Order has been demonstrated in a fairly large number of species [2] by Petersen, Lotar, A. Fischer, Potter, and Schenck, since this character was first discovered by Th. Hartig in *Cucurbita Pepo*. A remarkable point is the absence of this anatomical feature in two or three genera, which are very naturally included within the limits of the Order on account of their exomorphic and endomorphic characters; these genera are *Alsomitra*, *Gerrardanthus*, and *Anisosperma*. Petersen, as also A. Fischer and Hérail, were unable, in spite of very careful examination, to discover any groups of phloem at the inner margin of the vascular bundles in *Alsomitra sarcophylla*, Roem.; H. Schenck also failed to find them in *Anisosperma Passiflora*, Manso, and A. Fischer in a species of *Gerrardanthus*, the name of which is not given. According to my own observation, *Feuillea cordifolia*, L. and *Gynostemma integrifolia*, Cogn., which, however, were only examined in dried material, also appear to be without internal soft bast, and in *Zanonia indica*, L., bicollateral structure does not, at any

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[1] According to Hérail the Cucurbitaceae alone, among the Orders in which intraxylary phloem is known, possess true bicollateral bundles. For only in this Order is the inner phloem regarded as primary in origin, i. e. as proceeding from the same strand of meristem as the primary wood and bast. That the intraxylary phloem belongs to the vascular bundle is also indicated by the fact that the inner soft bast borders directly on the group of primary wood.

[2] These belong to the following genera, which are here taken as defined by Cogniaux in his Monograph: *Trichosanthes*, *Lagenaria*, *Thladiantha*, *Momordica*, *Luffa*, *Ecballium*, *Bryonia*, *Bryonopsis*, *Cucumis*, *Citrullus*, *Benincasa*, *Coccinia*, *Cucurbita*, *Wilbrandia*, *Melothria*, *Kedrostis*, *Maximowiczia*, *Cucurbitella*, *Abobra*, *Echinocystis*, *Cyclanthera*, *Sicyos*, *Sicyosperma* and *Microsechium*. To these I am able to add ***Actinostemma tenerum***, Griff. (tribe Gomphogyneae) from my own investigation.

rate, extend to all the bundles. The genera mentioned above, which have or appear to have simple collateral bundles, belong to the tribes Gynostemmeae, Zanonieae, and Feuilleae.

The vascular bundles are inserted as isolated strands in the ground-tissue of the stem and are separated from one another by broad radial strips of ground-tissue, which may be described as primary medullary rays. The bundles are, as a rule, arranged in two rings, but may be referred to a single ring of bundles, which usually project alternately towards the exterior and interior. Typically each of the two rings contains five vascular bundles corresponding to the cross-section of the stem, which usually has five angles. Occasionally, however, a different number of bundles may occur, as is shown by the following statements of Petersen (cf. next paragraph) and others of a similar kind in Lotar's work. Great systematic value should not, however, be attributed to the number of the vascular bundles, because various deviations occur in the different internodes of the same shoot.

Bryonia alba has seven outer and five inner vascular bundles. *Cucurbita Pepo*, *C. Melopepo*, *Citrullus edulis*, *Echinocystis lobata*, *Momordica Charantia*, *Lagenaria vulgaris*, *Eopepon vitifolius*, *Benincasa cerifera*, *Cucumis Colocynthis* have five outer and five inner bundles; the plants last mentioned, however, have some extremely small bundles in addition to the ten normally present. *Cucumis prophetarum*, *C. medullifera*, *Sicyospermum gracile*, *Thladiantha dubia*, *Rhynchocarpa africana*, and *Trichosanthes ovigera* have five bundles in the outer and four in the inner ring. *Alsomitra sarcophylla* has four bundles in each of the two rings. *Bryonopsis erythrocarpa*, *Cyclanthera elastica*, *C. pedata*, *Sicyos angulatus*, *Luffa amara*, *Coniandra dissecta*, *Momordica Balsamina*, *M. Huberi*, *Prasopepon Duriaei*, *Melothria Cucumis*, *M. pendula*, *Mukia scabrella*, and *Zehneria suavis* have five outer and three inner bundles; some of these plants have one or two additional bundles of soft bast. *Cucumis perennis* has 9 or 10 bundles arranged in two rings; each bundle, however, is accompanied by two smaller strands, which run on either side of and parallel to the larger bundles, and now and then fuse with the latter, especially in the neighbourhood of the nodes.

While the species, so far cited, show the vascular bundles arranged in two rings (at least in the young axis) the bundles in the round stem of *Ecballium agreste* are disposed in one ring only (De Bary). It has already been indicated above that the arrangement of the bundles in two rings becomes obliterated in those genera the bundles of which possess considerable secondary growth in thickness, such as Potter has described in *Cephalandra indica*, Naud., *Trichosanthes villosa*, Bl. and *T. anamalayana*, Bedd.; to these we may add the stems of *Wilbrandia verticellata*, Cogn. and *Anisosperma Passiflora*, Manso investigated by H. Schenck, as well as *Alsomitra sarcophylla* according to Hérail. In these species an interfascicular cambium is present, and by means of it the primary medullary rays are enabled to keep pace with the growth in thickness of the bundles. Interfascicular formation of wood and bast, however, does not take place in the plants (mentioned above) examined by Potter and H. Schenck. On the other hand, interfascicular development of wood and bast was observed by Hérail to occur locally in the herbaceous stem of *Lagenaria*. As regards the growth in thickness of the xylem in *Wilbrandia* and *Anisosperma*, it may be mentioned that in the thickened stems the segments of the wood form longitudinal plates, broadening outwards, and, together with their respective phloem-groups, become divided dichotomously by secondary medullary rays, which are similar to and of the same breadth as the primary rays.

The wood contains vessels with very wide lumina (reaching ·38 mm. in diameter) and simple perforations; in *Wilbrandia* and *Anisosperma* there are also tracheides, as well as simple wood-fibres. The phloem-groups

are characterized by sieve-tubes with wide lumina; the structure of these elements has repeatedly formed the subject of investigations (Th. Hartig, Nägeli, Wilhelm, A. Fischer, &c.). The internal soft bast sometimes shows secondary thickening, and in *Wilbrandia verticellata*, according to H. Schenck, it presents a peculiarity which, in older stems than those hitherto examined, may perhaps lead to a complicated anomalous structure; in two of the inner strands of phloem, in a piece of the stem of this species, H. Schenck observed a small strand of xylem; these two xylem-strands are of secondary origin, and arise through the activity of the cambium belonging to the inner phloem.

In the outer **cortex**, Petersen first described the occurrence, in the species investigated by him, of a sclerenchymatous ring consisting of prosenchymatous elements. This ring of sclerenchyma, which is usually continuous and often has an undulating course in the transverse section of the branch (corresponding to the projecting vascular bundles), appears to be present in all the herbaceous members of the Order which do not exhibit any considerable amount of growth in thickness. In those species, on the other hand, which form a woody stem, the sclerenchymatous ring is wanting, since in this case mechanical support is afforded by the ring of wood; e.g. in the species investigated by Potter and H. Schenck, already quoted several times. In these species the sclerenchymatous ring is replaced by small isolated bundles of sclerenchyma-fibres. The ring of sclerenchyma in the herbaceous species either borders directly on the phloem or is separated from the latter by a variable number of cell-layers belonging to the pericycle.

Formation of cork is rare (*Zanonia indica*, L.), and has only been observed in relatively thick stems; the cork arises in the primary cortex.

The sieve-tubes which occur outside the vascular bundles are of special interest to systematists and others. They were first observed by Sanio, and subsequently by certain other investigators; thus De Bary described the occurrence of sieve-tubes situated in the cortical parenchyma outside the ring of vascular bundles, as a constant feature in thick stems of members of this Order (*Cucurbita*, *Lagenaria*, *Cucumis*, *Ecballium*); again in *Cucurbita*, *Lagenaria*, and *Zehneria* Petersen recognized the series of sieve-tubes uniting the phloem-groups of neighbouring bundles; and lastly, J. E. Weiss has given an account of the occurrence of scattered groups of phloem in the stem of *Cucumis perennis*. We owe an accurate investigation of the features in question to A. Fischer. Apart from the sieve-tubes of the vascular bundles, A. Fischer distinguishes: firstly, ' hypodermal or ectocyclic ' sieve-tubes, that is those which are present between the epidermis and the ring of sclerenchyma; secondly, ' entocyclic ' sieve-tubes, situated on the inner side of the ring of sclerenchyma, but not belonging to the inner or outer sieve-tubes of the vascular bundles; and lastly, ' commissural sieve-tubes,' which unite the different kinds of sieve-tubes with one another.

A. Fischer investigated twenty-eight species of Cucurbitaceae with regard to the distribution of sieve-tubes, and distinguishes the following six types:

1. *Alsomitra*-type: vascular bundles of the simple collateral type, without commissural sieve-tubes and without ectocyclic or entocyclic sieve-tubes (*Alsomitra*. *Gerrardanthus*).

2. *Luffa*-type: vascular bundles bicollateral; protophloem-sieve-tubes alone occur, appearing at the outer limit of the procambial strands, situated opposite the angles of the internode, and lying on the inner side of the rudiment of the sclerenchymatous ring; they may be referred to the vascular bundle-system, or may be described as entocyclic sieve-tubes (*Luffa*, *Momordica*, *Trichosanthes*, *Thladiantha*, *Bryonopsis*).

3. *Bryonia*-type: vascular bundles bicollateral; numerous entocyclic sieve-tubes present; ectocyclic and commissural sieve-tubes are absent (*Bryonia*).

4. *Cyclanthera*-type: vascular bundles bicollateral; numerous entocyclic sieve-tubes, connected with one another and with the sieve-tubes of the vascular bundles by means of few commissures; no ectocyclic sieve-tubes (*Melothria, Cyclanthera, Coniandra, Rhynchocarpa, Cephalandra, Abobra, Maximowiczia, Ecballium, Colocynthis*).

5. *Lagenaria*-type: vascular bundles bicollateral; numerous entocyclic sieve-tubes and an abundant network of commissures; no ectocyclic sieve-tubes (*Citrullus, Benincasa, Coccinia, Sicyos, Sicyosperma, Microsechium, Cucumis, Lagenaria*).

6. *Cucurbita*-type: vascular bundles bicollateral; ectocyclic and entocyclic sieve-tubes as well as an abundant network of commisures (*Cucurbitella, Wilbrandia, Cucurbita*).

3. **Structure of the root.** Some members of the Order have roots with anomalous structure. These are: *Cucurbita*, according to Van Tieghem and Fischer; *Thladiantha dubia*, Bge., according to Dutailly, and Scott and Brebner; *Bryonia*, according to Stahl and J. E. Weiss; and *Ecballium Elaterium*, according to Van Tieghem, Morot, and Avetta. *Cucurbita* is distinguished by the occurrence of islands of soft bast situated in the wood and connected with the intraxylary phloem of the axis. In *Thladiantha dubia*, bundles of phloem (i. e. interxylary phloem) occur *in the radial rays of unlignified parenchyma, which characterize the wood of the root* in this species; some of these phloem-bundles are formed by the cambium on its inner side, but others arise secondarily as new formations; there is every probability that they are also in part connected with the intraxylary phloem of the stem. In *Bryonia dioica* cambial tissue is formed around individual groups of secondary vessels belonging to the wood of the root; this tissue produces xylem (without vessels) towards the centre, and phloem on the side away from the centre of the group of vessels concerned; hence concentric vascular bundles are formed in the wood. *Ecballium Elaterium* possesses quite a different anomaly, namely, successive rings of growth; the secondary zones of growth arise in an extra-fascicular position in the pericycle; in addition to this a secondary pith is formed in this plant by dilatation, and inversely orientated vascular bundles are developed at the margin of this pith. Finally, it may be mentioned that the thicker roots of the Cucurbitaceae frequently possess a pith containing intraxylary groups of soft bast, which subsequently may become converted into inversely orientated vascular bundles (Van Tieghem).

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BEGONIACEAE.

1. Review of the Anatomical Features. In all cases the stomata are found exclusively on the lower side of the leaf; the guard-cells are invariably surrounded by 3–6 subsidiary cells, which are arranged in one or two circles. The association of several stomata, together with their subsidiary cells, to form groups (Fig. 87, *A*) is characteristic of certain species only. The vascular bundles of the axis are isolated, being separated from one another by strips of lignified prosenchymatous tissue or thin-walled parenchyma. The xylem contains wood-prosenchyma with simple pits, wood-parenchyma and vessels having a kind of scalariform bordered pitting. The perforations of the vessels are simple as well as scalariform, and in the latter case have numerous bars; scalariform and simple perforations are sometimes found combined on the same division-wall of the vessel (Fig. 89, *A–B*). The epidermis of the axis, like that of the leaf, is usually many-layered. In the veins of the leaf, in the petiole and in the outer cortex of the axis typical collenchyma is of frequent occurrence. Medullary or cortical vascular bundles are only present in certain cases. In the same way the occurrence of branched spicular cells in the leaf (Fig. 87, *B*) and of mechanical elements accompanying the vascular bundles in the axis and leaf are only of importance for specific diagnosis. Oxalate of lime is excreted in forms belonging to the tetragonal system, and occurs as solitary crystals of various shapes and also as clustered crystals. Cystolith-like structures (cystotyles and cystospheres, Fig. 87, *C–E*), which occur in pairs corresponding to the well-known double cystoliths, are for the most part of systematic importance for certain sections of genera. Lastly, the structure of the hairs (Fig. 88) is exceptionally varied. The following types occur: ordinary uniseriate hairs, multiseriate shaggy hairs with varied structure, two-armed shaggy hairs, stellate hairs, tufted hairs, small scales, as well as short- and long-stalked glandular hairs with various types of structure in the stalk and head.

2. Structure of the Leaf. The leaf-structure was very thoroughly examined by Fellerer; his statements, which I repeat briefly below, are based on the investigation of no less than 282 species. It is impossible in this book, owing to limited space, to enumerate all the species in which the individual anatomical characters occur, and I must therefore let a few examples suffice, referring the reader to Fellerer's treatise for further information.

The **epidermal cells** of the leaf have relatively large lumina (mean superficial diam. = ·06 mm.), and as a rule possess straight lateral walls, in rare cases slightly, but never strongly undulated; the cells have approximately the same structure on both sides of the leaf. The size of the epidermal cells, or rather their superficial diameter, may sometimes be employed either for the recognition of certain sections of genera or in the diagnosis of individual species within the same section. Formation of papillae on the epidermis of the upper side of the leaf is very widely distributed; it occurs in about one-eighth of the species examined by Fellerer, but it is not of systematic value for large groups of species, and can only be employed with caution even for specific diagnosis, since papillae may sometimes be present and sometimes absent in the same species. The presence of papillae on the lower epidermis of the leaf is relatively rare (*Begonia heracleifolia*, Cham. et Schlecht. and other species). The walls of the epidermal cells are mostly very thin. The cuticle is likewise very thin, mostly granular (e.g. in *Begonia Balmisiana*, Ruiz and other species) or striate (*B. bulbillifera*, Link et Otto) or with irregular verrucose thickenings (*B. Karwinskyana*, A. DC. and other species). The vertical angles of the epidermal

cells are commonly distinguished by collenchymatous thickening (e.g. in *B. Cumingiana*, A. DC. or *B. subvillosa*, Kl.). The cell-sap of the epidermal cells is most commonly colourless, though it may often be coloured red on the lower side of the leaf (in species inhabiting virgin forests).

Beneath the epidermis in very many cases (in 121 species among the 282) a one- or many-layered **hypoderm** occurs; it is usually present on both sides, as for example in the section *Gireoudia*, more rarely only on one side of the leaf; in the latter case it occurs much more frequently on the upper (e.g. in the section *Scheidweileria*) than on the lower side (in the section *Eupetalum*). Developmentally this hypoderm belongs to the integumental tissue, according to Pfitzer's investigation. The hypodermal cells as seen in surface-view are mostly distinguished by the large size of their lumina (diam. = ·043–·2 mm.); in consequence of this the hypoderm may often be recognized on the upper side of the dried leaf as a delicate network with distinct meshes. The vertical angles of the hypodermal cells are commonly thickened like collenchyma.

The **stomata** are found exclusively on the lower side of the leaf, and are never present in very great numbers. In this Order each pair of guard-cells is surrounded by 3–6 subsidiary cells, which are mostly thin-walled; of these, three form an inner ring, around which the remainder, when present, are grouped. According to Strasburger, the course of development of this stomatal apparatus is the same as in the Crassulaceae. That is to say, the initial cell divides by successive vertical walls, running in three directions, so as to produce, besides the mother-cell of the guard-cells, a single or double belt of subsidiary cells surrounding it. The whole stomatal apparatus consisting of a pair of guard-cells with its subsidiary cells may either be inserted in the epidermis, or may have the whole or part of its margin resting upon it. On the basis of these features Fellerer distinguishes the following types: a flush ('eingeklemmt') stomatal apparatus, and also the suspended ('eingehängt'), overlapping ('übergreifend'), half-flush ('halbseitig eingeklemmt'), and half-suspended ('halbseitig eingehängt') types, these being characteristic of certain species. The stomata are either solitary or united into groups. The groups of stomata (Fig. 87, *A*) are mostly recognizable even with the naked eye as white dots or spots, and can be employed for systematic purposes. Fellerer distinguishes overlapping ('übergreifende') stomatal groups from such as do not overlap. The former lie with their margins upon the epidermis; the latter are on the same level as the rest of the epidermal cells. Before leaving the subject of stomata the water-pores may be mentioned. They occur now and then on the upper side of the leaf near the margin.

The **mesophyll** of the leaves is usually composed of palisade-tissue, which is invariably one-layered, and of spongy tissue, one or more layers in thickness. In rare cases (*B. alchemilloides*, A. DC. and other species) the mesophyll consists of ordinary parenchymatous tissue only. The palisade-cells, when elongated, commonly show a concertina-like folding of the lateral walls; when short, they become narrower inwards and have a conical form. In most cases the palisade-cells fit closely together. The 'silver spots' on the leaves of the Begoniaceae are due to the fact that the palisade-tissue is locally interrupted, and is replaced at these points by spherical cells, which have the characters of the spongy tissue, and are surrounded by intercellular spaces containing air. A differentiation, which is especially worthy of mention, is shown by a certain number of the palisade-cells in *Casparya grewiaefolia*, A. DC., *C. trachyptera*, A. DC., and *C. Urticae*, A. DC. *B. hispida*, in which these cells are developed like stone-cells; in those of *Begonia conchaefolia*, Dietr., the upper wall, as well as the upper half of the lateral walls, is thickened.

The spongy tissue presents no special features; the intercellular spaces are usually small, but in rare cases they may be large. As special elements of the mesophyll branched spicular cells (Fig. 87, *B*) appear in certain *Begonias* which are very closely related to one another; these cells are of various shapes, with a pitted wall of varying thickness, and their lumen sometimes contains a crystal of oxalate of lime. Spicular cells were observed by Fellerer in *Begonia angularis*, Raddi, *B. arborescens*, Raddi, *B. stenophylla*, A. DC., *B. paleata*, A. DC., *B. parvipeltata*, A. DC., and *B. fruticosa*, A. DC.

With regard to the structure of the veins, it may be remarked that the ground-tissue of the larger veins often contains strongly developed and typically differentiated collenchyma beneath the epidermis, and that the vascular bundles in certain species are accompanied by special mechanical tissue. The latter consists of elongated sclerenchyma, which is either of the nature of

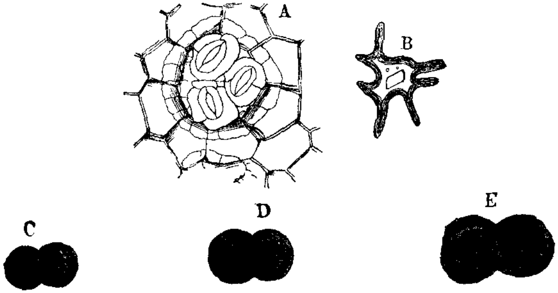


FIG. 87. A, Stomatal group of *Casparya fuchsiaeflora*, A. DC. B, Branched spicular cell from the leaf of *Begonia arborescens*, Raddi. C, Double cystotyle of *B. luxurians*, Hort. Monac. D, Double cystotyle of *B. paleata*, A. DC. after treatment with alcohol. E, Double cystosphere of *B. laetevirens*, Van Houtte.—After Fellerer.

prosenchyma or parenchyma. Sometimes also wide-lumened stone-cells occur in the neighbourhood of the vascular bundles.

The **hairy covering** is exceptionally varied and is suitable for employment in specific diagnosis. Fellerer distinguishes two main classes of trichomes: (1) hairs in which a head is not present, and (2) capitate hairs.

The hairs of the first type are always multicellular, and in the simplest case are ordinary uniseriate hairs. The latter are connected with the multiseriate shaggy hairs by transitional forms. A special form of shaggy hair is that in which the outermost cells of the hair have free mammilliform tips, and stand out from the hair like the scales of an open Coniferous cone (Fig. 88, *A*). Another special form is found in *Begonia monadelpha*, Ruiz et Pav., *B. parviflora*, Poepp. et Endl. (Fig. 88, *B*), *B. muricata*, Scheidw. and other species, in which the shaggy hair is reduced to a few cells and becomes a shortly spinous, star-like structure. Two-armed shaggy hairs sometimes occur (*Begonia solananthera*, A. DC., Fig. 88, *C*); in these the portion forming the arms consists of several rows of cells. If we imagine the arm-portion in the preceding type extended to form a one-layered plate of cells, we can associate with it those superficially extended or scale-like structures, which usually have a fusiform outline and occur in *B. xanthina*, Hook., *B. ovatifolia*, A. DC. and *B. solananthera*, A. DC. Again, the transitions from shaggy hairs to true emergences

are interesting; the parenchyma, situated beneath the epidermis, contributes to the formation of these hairs, which are stiffened by sclerenchymatous prosenchyma-cells. The emergences in question were first described by Haberlandt in *Begonia imperialis*, Lem. var. *smaragdina*, and were also demonstrated by Fellerer in *B. nelumbiifolia*, Cham. et Schlecht., *B. pustulata*, Liebm. and *B. violaefolia*, A. DC. Another type of hair, in which no head is present, has been termed by Fellerer a whip-like hair (Fig. 88, *D*). He means by this term very long (up to 2 mm. or more) and at the same time very narrow hairs (breadth scarcely above ·03 mm.), in which one can distinguish a kind of whip-handle, a basal portion and a long lash-like terminal portion. The basal and terminal portions may consist of one row of cells, or the basal portion may be

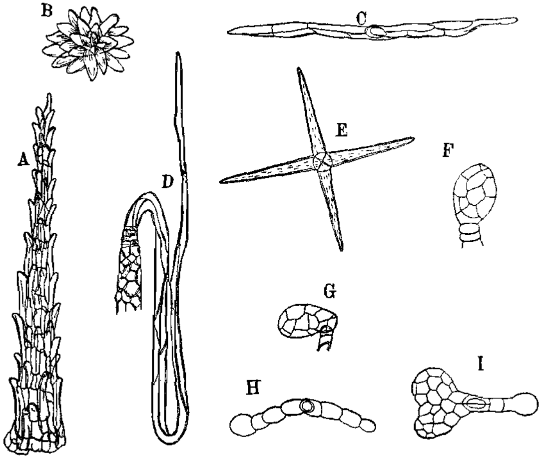


FIG. 88. Forms of trichomes of the Begoniaceae: A, *Begonia hispida*, Schott; B, *B. parviflora*, Poepp. et Endl.; C, *B. solananthera*, A. DC.; D, *B. sericoneura*, Liebm.; E, *B. sinuata*, Wall.; F, *B. pretoniensis*, Moore; G, *B. caroliniaefolia*, Reg.; H, *B. xanthina*, Hook.; I, *B. rhizocarpa*, Fisch.—After Fellerer.

uniseriate and the terminal portion multiseriate, or conversely the basal portion multiseriate and the terminal portion uniseriate, or lastly basal and terminal portions may both be multiseriate. Besides these there are stellate hairs (Fig. 88, *E*) with a stalk, which is usually unicellular and bears four arm-cells, spread out in one plane and placed at right angles to one another (*Begonia sinuata*, Wall.), and there are also shortly stalked tufted hairs with a uniseriate stalk and unicellular rays (*B. parvipeltata*, A. DC., and *B. grisea*, A. DC.).

Amongst the capitate hairs (glandular hairs, Fig. 88, *F–I*) we likewise meet with various types of differentiation, due to the diverse structure of the stalk and head. The head may consist of few or many cells, and may be spherical, ellipsoidal, club- or hammer-shaped. The stalk of the glandular hairs is either short and uniseriate or consists of a shaggy hair, which varies in length and structure. With the glandular hairs we must also class the curious pearl-

glands, which were discovered by Meyen in *Begonia platanifolia* and *B. vitifolia*, and which also occur in *B. reticulata*. They are relatively large, spherical, multicellular vesicles, with quite a short stalk; they appear of an aqueous clearness, and fall off at the least touch; according to Penzig and Warburg, this latter feature suggests an investigation of a possible relation of these glands to ants (namely, as food-bodies). In consequence of their falling off so easily Meyen's glands are only exceptionally to be met with on herbarium material.

Amongst the contents of the cells in the tissues of the Begoniaceae, the crystals of **oxalate of lime** and the cystolith-like structures principally require mention. The crystals belong to the quadratic system, and either appear singly as octahedra, the shape of which may be like that of an envelope, or as quadratic prisms, combined with the octahedron. Now and then (e.g. in *Begonia cucullata*, Willd., *B. martinicensis*, A. DC., &c.) a kind of crystal-sand is found, in which larger solitary crystals are embedded. Side by side with the solitary crystals, clustered crystals occur, which are apparently composed of individuals of the quadratic system; transitional forms are also to be met with.

The **cystolith-like structures** (Fig. 87, *C–E*), occurring in certain members of the Order, require a more detailed discussion; they were first met with by Hildebrand in the pith of some Begoniaceae, and later on, especially by Radlkofer, in the leaf-parenchyma of certain species. They are differentiated in two adjoining cells as a kind of double-cystolith, each half having an approximately hemispherical shape, and they commonly give rise to transparent dots in the leaf. In accordance with their diverse appearance, which corresponds to variations in structure and chemical composition, Fellerer distinguishes three forms:

I. Cystolith-like structures (Fig. 87, *C*), which appear as white, translucent bodies in dry sections exposed to the air, and swell up in water into a transparent, apparently structureless mass. If the swollen masses are treated with alcohol, they contract and come to resemble the decalcified double-cystoliths of '*Momordica echinata*' (see Penzig, in Bot. Centralblatt, viii. 1881, Tab. ii, Figs. 3 and 5), showing distinct concentric stratification about the centre of the common division-wall of the containing-cells as well as radial striation; in the middle of the division-wall a refractive body is discernible, which on closer observation proves to be a pit, into which the mass of the cystolith extends like a stalk. On fresh addition of water these stratified cystolith-like masses can again be made to swell up and thus to apparently disappear; renewed treatment with alcohol once more makes them stand out clearly. In the first form of the cystolith-like bodies of the Begoniaceae (which Fellerer, following Radlkofer's example, comprises together with the second form to be discussed below, under the name of cystotyles), judging only by appearance and reactions, we are thus concerned with double cystoliths, which possess no crystalline infiltration, but consist solely of a framework, metamorphosed into mucilaginous substance. The supposition which suggests itself, that the form of cystolith under discussion develops in the same way as the cellulose framework of the ordinary cystoliths, and that the transformation of the cellulose substance into mucilage may only take place subsequently, has not been confirmed by Fellerer's investigations of the development, into which we cannot enter further here; according to him the appearance of the mucilage is a primary phenomenon.

II. The second form of the cystolith-like bodies, which Fellerer, as already stated, also describes as cystotyles, and which correspond to the 'resinocysts' of Schoenett, exhibits a finely granular structure and yellowish refraction of the light in dry sections exposed to the air; they become grey on the addition

of water, and at the same time the granular structure and stratification appear distinctly. The latter appearance is also presented by these structures in the living plant. So far as outward appearance is concerned these bodies recall the spherical thickenings of the cell-wall in the root-cap of *Sobralia* and other Orchideae, which were described by Leitgeb (Sitz.-Ber. der Wien. Akad., Bd. XLIX. 1. 1864, p. 275 et seq.). Alcohol deprives this second form of cystotyle of the infiltrated substances, which, according to the various reactions employed by Fellerer, are of a resinous nature. According to Fellerer, the structure remaining after treatment with alcohol [1] is, to put it shortly, a kind of cystotyle of the first type, which shows the stratification, but, like the former, swells up with water, so that it apparently disappears; it can again be obtained in the stratified form by a fresh exposure to alcohol.

III. Finally, the third form of the cystolith-like structures occurring in the Order, termed **cystospheres** (Fig. 87, *E*) by Fellerer, appears as whitish-yellow or brownish, strongly refractive, brittle, gelatinous masses in sections mounted dry or in water, and, in the living plant, as liquid, brightly shining, dull white or yellow masses of secretion, which are enclosed in a special sac. The secretion is of a resinous nature, but does not appear to consist of a uniform substance.

With regard to the course of development of the structures in question, reference should be made to the works of Fellerer and Schoenett.

Fellerer has shown by a study of the development of the three forms discussed above that they may be classed together and interpreted as cystolith-like structures, and that they may be regarded as corresponding to the double cystoliths of *Momordica*. This conclusion is of importance from a systematic point of view, because it casts new light on the relationships of this Order to the Cucurbitaceae.

With regard to the occurrence of the cystotyles and cystospheres in the various vegetative and reproductive organs of any one plant, there is a great degree of variation, as Fellerer has shown. The investigations on this point have nevertheless demonstrated the fact that, when no cystolith-like structures occur in the leaf, they are altogether wanting in the plant, and therefore conversely that, when cystolith-like structures are present in any member of the Order, they are invariably met with in the leaf-tissue. The cystotyles and cystospheres have been observed in the leaf both in the palisade and spongy tissue of the mesophyll; they are occasionally found in the hypoderm and in the shaggy hairs, but never in the epidermis itself.

With respect to the distribution and systematic value of the structures in question, we may first mention that Fellerer met with them in 59 species. Their detailed differentiation is of specific value. Still more important, however, is the fact that the occurrence of cystolith-like structures is in most cases a sectional character, and thus serves as a test for a natural group of species. The only essential exception is afforded by the section *Ruizopavonia*, which includes species with and without cystoliths, and altogether forms a very questionable natural specific group. It further appears that the sections which possess cystolith-like structures are also closely related to one another. Thus, for example, the sections *Pritzelia, Wageneria, Philippomartia, Scheidweileria, Ewaldia, Trendelenburgia* and *Steineria*, which are regarded as very closely related by De Candolle on the ground of his exomorphic studies, without exception possess cystotyles or cystospheres.

The cystolith-like structures of the Begoniaceae have been observed by Fellerer in the following sections and species of the genus *Begonia* (in this enumeration, which follows the system of A. De Candolle, Cs. = cystospheres, Ct. = cystotyles): *Saueria*,

[1] The resinocysts of the species referred by Schoenett to *Begonia Evansiana* (?), give a cellulose reaction after the resin is removed.

Cs. (*B. sulcata*, Scheidw.); *Begoniastrum* pro parte, Ct. (*B. paulensis*, A. DC., *B. rubro-pilosa*, A. DC., and *B. Hilariana*, A. DC.); *Ruizopavonia* pro parte, Cs. (*B. glauca*, R. et P., *B. carpinifolia*, Liebm.); *Gireoudia* pro parte, Cs. (*B. urophylla*, Hook., *B. glandulosa*, A. DC., *B. involucrata*, Liebm., *B. laciniosa*, A. DC., *B. broussonetiaefolia*, A. DC., *B. multinervia*, Liebm.); *Pritzelia*, Ct. (*B. ramentacea*, Paxt., *B. princeps*, Hort. Berol., *B. sanguinea*, Raddi, *B. Riedelii*, A. DC., *B. angularis*, Raddi, *B. angulata*, Vell., *B. coccinea*, Hook., *B. Fischeri*, Otto et Dietr., *B. bahiensis*, A. DC.); *Wageneria*, Ct. + Cs. (*B. stenophylla*, A. DC., Ct., *B. polygonifolia*, A. DC., Cs., *B. epibaterium*, Mart., Cs., *B. fagifolia*, Fisch., Cs., *B. smilacina*, A. DC., Cs., B. *scandens*, Sw., Cs., *B. hispida*, Schott Ct., *B. palcata*, A. DC., Ct., *B. neocomensium*, A. DC., Cs., *B. acida*, Mart., Ct., *B. Gardneri*, A. DC., Cs., *B. Hügelii*, Hort. Berol., Cs., *B. sylvatica*, A. DC., Ct., *B. convolvulacea*, A. DC., Cs., *B. longipes*, Hook., Cs., *B. vitifolia*, Schott Cs., *B. dichotoma*, Jacq., Cs., *B. scabrida*, A. DC., Cs., *B. Saxifraga*, A. DC., Cs., *B. peltata*, A. DC., Cs., *B. parvipeltata*, A. DC., Ct.; cystolith-bodies have not been observed in *Begonia dominicalis*, A. DC., *B. grisea*, A. DC. and *B. parvipeltata*, A. DC. var. *bahiensis*; according to Fellerer, *B. dominicalis* must, however, be transferred to the section *Begoniastrum* and is perhaps identical with *B. dominicensis*, Herb. Monac., *B. grisea* has already been recognized by A. De Candolle as belonging doubtfully to the section *Wageneria*; *B. parvipeltata*, var. *bahiensis*, is, according to Fellerer, certainly no variety of *B. parvipeltata*, and perhaps forms a new section together with *B. grisea*); *Philippomartia* Ct. (*B. neglecta*, A. DC., *B. membranacea*, A. DC.); *Scheidweileria*, Ct. (*B. parviflora*, Poepp. et Endl., *B. muricata*, Scheidw., *B. luxurians*, Lem., *B. digitata*, Raddi, *B. inciso-serrata*, A. DC.); *Ewaldia* Ct. (*B. lobata*, Schott, *B. tomentosa*, Schott, *B. rigida*, Reg., *B. Boucheana*, A. DC., *B. rutilans*, Hort. van Houtte); *Trendelenburgia*, Ct. (*B. fruticosa*, A. DC.); *Steineria*, Ct. (*B. arborescens*, Raddi, *B. Hookeriana*, Gardn., *B. oxyphylla*, A. DC., *B. dentatiloba*, A. DC., *B. sylvestris*, A. DC., *B. bidentata*, Raddi, *B. Schottiana*, A. DC.); Species dubia: *B. parvifolia*, Schott Ct.

Regarding the structure of the **petiole** it may be briefly mentioned that its vascular bundles are isolated, and that the occurrence of medullary bundles in the petiole together with other features, such as the occurrence or absence of mechanical tissue-elements, may, according to Duchartre and Fellerer, be employed in specific diagnosis.

3. Structure of the Axis. For our knowledge of the structure of the axis in this Order we are chiefly indebted to the investigations of Hildebrand. The epidermis of the axis consists of 1–4 layers. Where cork occurs, it arises, according to Hildebrand, immediately below the epidermis, according to Duchartre sometimes in the epidermis itself. Internal to the epidermis and the hypoderm one meets with 3–8 cell-layers of more or less typically differentiated collenchyma. This is followed by thin-walled tissue containing crystals and chlorophyll, or sometimes with red cell-sap. The **vascular bundles** of the normal ring are either isolated, being separated by ground-tissue, or form a more or less closed ring. In the upright, shrubby species the ground-tissue, running between the vascular bundles in the radial direction, consists of elongated cells which have lignified walls and slit-shaped pits, and belong rather to the prosenchymatous type, whilst in some root-climbers (*B. fruticosa*, A. DC., *B. convolvulacea*, A. DC., and *B. catharinensis*, Taub.), according to H. Schenck, the cells of this tissue are radially elongated in the ordinary way or are isodiametric and thin-walled, forming broad medullary rays of the Aristolochiaceous type. The xylem of the vascular bundles, apart from the primary vessels, is composed of simple-pitted, sometimes delicately septate wood-prosenchyma, of wood-parenchyma and pitted vessels. Where the latter come into mutual contact, they bear scalariform bordered pits. The perforations of the vessels vary greatly; thus simple circular perforations occur, as well as others which are scalariform with many bars, and thirdly combinations of the two forms (Fig. 89, *A–B*). Two of these forms may occasionally be present at the ends of the same component cell of a vessel—a different type occurring at either end. The mechanical tissue commonly

accompanying the bast of the bundles on its outer side, consists both of elongated parenchymatous elements and of prosenchymatous cells with slit-shaped pits. The **pith** is formed of large, parenchymatous cells with thin, pitted walls.

The occurrence of cortical and medullary vascular bundles is a noteworthy feature in certain members of the Order. The **cortical bundles** are confined to a few species (*Wageneria tomentosa*, Kl. and *Pritzelia zebrina*, Kl.); according to Hildebrand they arise in each node from the normal ring of bundles, run vertically upwards through the cortex as isolated strands, and usually pass out into the leaf at the next node above. The **medullary vascular bundles** are more widely distributed. Hildebrand met with them in 28 of the 128 species which he examined. Hildebrand's investigations have shown that the occurrence of these medullary bundles is only of importance in specific diagnosis, and that it cannot be employed in the delimitation of natural groups of species. Westermaier attempted to give a physiological explanation of Hildebrand's and his own results regarding the occurrence or absence of medullary vascular bundles in this Order, but did not meet with success (see loc. cit.). In dealing with the course of the medullary bundles of the Begoniaceae, Hildebrand, Sanio, and Westermaier came to the conclusion that these bundles are in great part cauline. On the other hand, J. E. Weiss supports the leaf-trace nature of the medullary bundles, basing his view on Westermaier's work. He shows that the bundles which have been stated to be cauline, enter the ring of bundles at the node and at a still higher node bend out into the leaf. The structure of these bundles is collateral in some cases, in others it shows a tendency towards concentric differentiation with central phloem (Möbius).

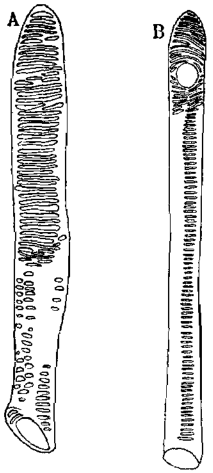


FIG. 89. Segments of vessel, some of which have composite perforations: A, *Gurltia Boucheana*; B, *Begonia Hügelii*.—After Hildebrand.

The species with medullary bundles may be enumerated here for the use of the systematist. Klotzsch's nomenclature, which was adopted by Hildebrand, is employed: *Knesebeckia discolor*, Kl., *K. ignea*, Kl.; *Gurltia Boucheana*, Kl.; *Nephromischus rutilans*, Kl.; *Scheidweileria muricata*, Kl., *S. luxurians*, Kl., *S. digitata*, Kl., *S. inciso-serrata*, Kl.; *Steineria ferruginea*, Kl., *S. pulchella*, Kl.; *Gireoudia involucrata*, Kl., *G. laciniata*, Kl., *G. crassicaulis*, Kl., *G. caroliniaefolia*, Kl.; *Pritzelia zebrina*, Kl.; *Wageneria tomentosa*, Kl.; *Platycentrum rubrovenium*, Kl., *P. xanthinum*, Kl.; *Cladomischus annulatus*, Kl., *C. Roylei*, Kl.; *Sphenanthera robusta*, Hassk.; *Begonia acerifolia*, Hort. Berol., *B. glaucescens*, Hort. Berol., *B. Hügelii*, Hort. Berol., *B. platanifolia*, Hort. Berol., *B. Rex*, Hort., *B. Simonsii*, Hort. Low.

Literature: Meyen, Sekretionsorg., Berlin, 1837, p. 45.—Hildebrand, Anat. Unters. üb. die Stamme d. B., Berlin, 1859, 34 pp. and 8 Tab.—Sanio, in Bot. Zeit. 1864, p. 224.—Strasburger, Spaltöffn., Pringsheim Jahrb., Bd. v, 1866-1867, p. 323.—Pfitzer, Mehrsch. Ep. etc., Pringsheim Jahrb., Bd. viii, 1872, p. 31 et seq. and Tab. vi.—De Bary, Vergl. Anat., 1877.—Westermaier, Markst. Bündelsyst. d. B., Flora 1879, 24 pp. with 2 Tab.—J. E. Weiss, Markst. Bündelsyst., Bot. Centralbl. 1883, iii, p. 287 et seq. and Tab. i.—Solereder, Holzstr., 1885, pp. 140, 141.—Haberlandt, Zur Anat. d. B., Mitteil. naturw. Ver. f. Steiermark, Graz, 1887, 12 pp. and 1 Tab.—

Möbius, Konzentr. Gefässb., Ber. deutsch. bot. Gesellsch. 1887, pp. 12, 13.—Petit, Pétiole, Mém. Soc. sc. phys. et nat., sér. 3, t. iii, 1887, p. 325 and pl. v.—Duchartre, Obs. sur le sous-genre *Lemoinea*, E. Fourn., Paris, 1889, Topogr. Gaston Née, 100 pp. and 2 pl.—Radlkofer, in Sitz.-Ber. Münch. Akad. 1890, pp. 115-18.—Fellerer, Beitr. z. Anat. u. Syst. d. B., Diss., München, 1892, 239 pp. and 3 Tab.—Benecke, Nebenz. d. Spaltöffn., Bot. Zeit. 1892, pp. 554, 555.—Penzig, Perldrüsen, *Atti del Congr. bot. internaz. di Genova*, 1892, p. 240 and Tab. xv.—H. Schenck, Anat. d. Lianen, 1893, pp. 149-51.—Warburg, in Natürl. Pflanzenfam., iii. Teil, Abt. 6 a, 1894, pp. 125-7 and Fig. 46.—Stahl, Bunte Laubbl., Ann. Jard. bot. de Buitenzorg, vol. xiii, 2, p. 137 et seq. and pl. xvii.—Wittlin, Kalkoxalattasch., Bot. Centralbl. 1896, iii, p. 160.—Zalewski, Schoenett's Resinocysten, Bot. Centralbl. 1897, ii, pp. 50-5 (discussion of Schoenett's treatise in Kosmos, Org. d. poln. Naturf. Ver. Kopernik in Lemberg, Bd. xviii, p. 382).

DATISCEAE.

Of this small Order, which includes three genera with five species, only *Datisca cannabina*, L. and *Octomeles sumatrana*, Miq.[1] were available for investigation.

Regarding the structure of the **leaf**, the following points should be mentioned. The leaf-structure is bifacial in both species. The stomata, which only in the case of *Octomeles sumatrana* occur on both sides (though in small numbers on the upper side) are surrounded by several epidermal cells. In *Octomeles sumatrana* a one-layered hypoderm is developed beneath the upper epidermis; the mesophyll of this plant contains spicular cells, which are approximately H-shaped, and traverse the entire thickness of the leaf, whilst some of their arms penetrate as far as the cuticle on both sides. The vascular bundles of the veins are accompanied by mechanical tissue in *Octomeles sumatrana* only. Oxalate of lime has been observed in the form of small prismatic or needle-shaped crystals, especially in the leaf of *Octomeles*. The trichomes occurring in *Datisca* are glandular shaggy hairs, which are composed of a multiseriate stalk of variable length and of a spherical or ellipsoidal, multicellular, glandular head; the scale-hairs, which are found in *Octomeles*, have a quadriseriate stalk and a rather large, one-layered, circular shield with an entire margin; the cells of the shield have an approximately quadrangular shape in surface-view, and are arranged for the most part radially.

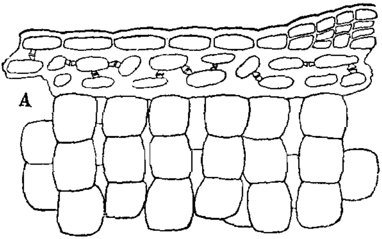
In the structure of the **wood** the two species investigated agree in the possession (*a*) of vessels with rather wide lumina and horizontal, transverse walls with simple perforations, (*b*) of wood-prosenchyma with wide lumina and simple pits, and (*c*) of narrow medullary rays. The vessel-walls where they are in contact with parenchyma of the medullary rays, show transitions to simple pitting in *Datisca*; in *Octomeles* bordered pitting is, at least in some cases, found in these regions, while the adjacent wall of the medullary ray is thickened in a well-marked reticulate manner. In *Datisca* the pericycle contains isolated bands of bast-fibres with wide lumina, in *Octomeles* a composite and continuous ring of sclerenchyma. Secondary groups of bast-fibres are present in *Octomeles*. In *Octomeles sumatrana* groups of stone-cells are found in the pith, and branched sclerenchymatous cells in the pith and primary cortex. The cork of *Octomeles* consists of cells with wide lumina and relatively thin walls.

CACTEAE.

The Cacteae, as is well known, constitute an Order which is distinguished from all others by its habit. Except in the species of the genus *Pereskia*, which have thick and fleshy leaves, foliage leaves of the ordinary form are wanting; for in the other genera a fleshy shoot, the structure of which is adapted to a desert-climate, appears immediately after the two normally developed cotyledons; this shoot takes over the function of the foliage leaves,

[1] For *Octomeles* see also Warburg, in Natürl. Pflanzenfam., iii. Teil, Abt. 6 a, 1894, p. 151.

and only bears very small foliar structures, some of which are transformed into thorns. The anatomical features of the Order, which will be described in the following pages from statements in the literature, present many points of interest, especially to the physiologist, who can readily correlate the structural features with their physiological causes in an Order of plants which (like the Cacteae) is adapted to quite special and uniform conditions of existence; the



anatomical features, however, are also of interest to the systematist, since all the investigations hitherto carried out have shown that many an anatomical feature can be employed in the grouping and diagnosis of the genera and species.

The **stomatal apparatus** is characteristic of the entire Order, as Schleiden first pointed out, and as has been confirmed by all the later authors. The guard-cells are accompanied on both sides by one or more subsidiary cells, parallel to the pore [1]. The occasional occurrence of a secondary division-wall, placed at right angles or obliquely to the pore in the one or the other subsidiary cell (as Benecke and others have remarked), is of course not to be regarded as an exception to the general type; the same applies to the complete suppression of the subsidiary cells on one side of the guard-cells; according to Caspari, this sometimes occurs in species of *Pereskia* and *Mammillaria*. The stomata are found in large numbers on the shoots of the Cacteae and also on the leaves in the species of *Pereskia*. The small rudimentary leaves in *Opuntia*, which fall off at an early date, also bear stomata; the latter, however, are abortive or anomalously developed. The stomata are commonly found at the base of saucer-like depressions on the

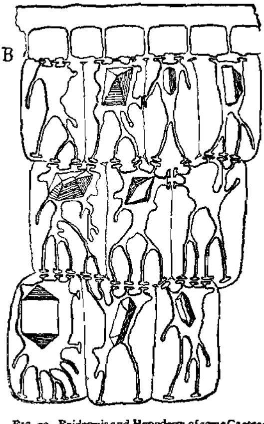


FIG. 90. Epidermis and Hypoderm of some Cacteae: A, *Cereus variabilis*; B, *Melocactus macrocanthus*.—After Schleiden.

[1] Developmental investigations have shown that in *Pereskia* the pair of guard-cells and the subsidiary cells arise by subdivision of the initial cell (Strasburger).

surface of the shoot, a feature evidently of advantage to desert-plants, which have to diminish transpiration as far as possible. Caspari mentions this as being quite general, and Vöchting records it in a few species of *Rhipsalis*. The direction of the pore of the guard-cells with reference to the longitudinal axis of the shoot is very noteworthy, and appears to be characteristic in certain genera. Thus in some of the genera (*Pfeiffera* and *Rhipsalis* according to Vöchting, *Echinopsis* and *Cereus* according to Lauterbach) the pore is placed at right angles to the longitudinal axis of the shoot, and is consequently horizontal; in another group of genera (*Lepismium* according to Vöchting, *Epiphyllum* and *Opuntia* according to Lauterbach) it is parallel to the longitudinal axis of the shoot, and is thus vertical, while in a third group (*Mammillaria Echinocactus* and *Phyllocactus* according to Lauterbach) the pore is irregularly orientated.

The **epidermal cells** of the shoots of the Cacteae, as Schleiden first noticed, have sometimes straight, sometimes undulated lateral walls. The cuticle, as also the entire external wall, varies in thickness; the former is often continued from the pore of the guard-cells over the entire wall of the respiratory cavity (Mohl). The cuticle is strengthened by the formation of cuticular ridges (*Echinocactus* according to Lauterbach) and thickened by a deposition of wax (in the form of a covering, which is either loose and readily rubbed off or firm and continuous, the former, e.g. in *Pilocereus Houlletii*, Lem. or *Cereus pruinosus*, S. Dyck, the latter in *Rhipsalis paradoxa*, S. Dyck or *Opuntia*, according to Schumann). The following special structural features of the epidermis remain to be mentioned: (*a*) the formation of furrows and ridges on the epidermis (species of *Rhipsalis* of the group *Teretes*, according to Vöchting), the stomata either occurring on the surface of the ridges (*R. conferta*, S. Dyck, *R. Cassytha*, Gaertn., *R. pendula*, Vöcht.) or in the furrows (*R. floccosa*, S. Dyck, *R. funalis*, S. Dyck); and (*b*) the appearance of relatively thin secondary division-walls in the epidermal cells (species of *Rhipsalis* according to Vöchting; *Echinopsis*, *Phyllocactus* and *Pereskia* according to Lauterbach). Beneath the epidermis there is a hypoderm (Fig. 90, *A–B*), which consists of one or more layers, and is mostly collenchymatous; it does not originate from the dermatogen, and must therefore be referred to the cortical tissue. According to Schleiden, the hypoderm either consists of a single row of cells (in *Cereus Curtisi* and probably in all *Mammillarias*) or of two rows of cells (*Cereus variabilis*) or of three or more (*Opuntia monacantha*, *Echinocactus Eyriesii*, *Melocactus macrocanthus*, *Cereus serpentinus* and *C. grandiflorus*). It is sometimes sharply marked off from the remaining tissue (*Cereus tetragonus* and *C. phyllanthoides*), sometimes not very distinctly delimited. The wall of the hypodermal cells is gelatinous and traversed by abundant, often branched pit-canals, which radiate out from the small lumen of the hypodermal cells and are sometimes enlarged into a narrow border at their extremity. The lumen of the collenchymatous hypodermal cells commonly contains crystals: for example clustered crystals, showing varied distribution in *Opuntia monacantha*, *O. brasiliensis*, and *O.* '*peruviana*,' solitary crystals in *Melocactus macrocanthus* and *Cereus Curtisi*.

In connexion with Schleiden's statements regarding the hypoderm of the Cacteae, it may be pointed out that Vöchting describes a one-layered hypoderm, which shows stronger thickenings at the corners, as occurring in *Pfeiffera cereiformis*, S. Dyck; a one-layered, somewhat thickened hypoderm in *Lepismium*; and a two-, rarely one-layered hypoderm in the species of *Rhipsalis*. According to Lauterbach, the hypoderm is one-layered and collenchymatous, or entirely suppressed in *Mammillaria*, 2–5 layered and collenchymatous in *Echinocactus*, 2–3 layered and collenchymatous in *Echinopsis*, 2–3 layered, but less collenchymatous in *Cereus*, two-layered in *Phyllocactus*, one-layered and collenchymatous in *Epiphyllum*, 1–2 layered and slightly collenchymatous in *Rhipsalis*, 2–4 layered and strongly collenchymatous in *Opuntia*,

but absent in *Pereskia*. The strongly developed collenchymatous hypoderm of *Melocactus*, which contains crystals, has been described in detail and figured by Van Breda de Haan. See also Michaelis' statements regarding this feature.

Cork-formation, so far as is known, is superficial in this Order. According to Schleiden, the cork originates in the epidermis or subepidermally, and consists (in *Opuntia monacantha* and *Echinocactus Eyriesii*) of alternating layers of cork-cells with thin and thick walls.

The **ground-tissue** of the stem is principally composed of ellipsoidal cells, which are separated by intercellular spaces of corresponding dimensions. In the neighbourhood of the epidermis and in the primary medullary rays the ground-tissue consists of more closely packed cells. In many species of *Rhipsalis* (for details see Vöchting) parenchymatous cells with thick walls are included in the ground-tissue. The cell-contents of the ground-tissue will be referred to below. The **vascular bundles** are in general arranged in a ring, quite in the normal way; in addition medullary or cortical bundles occur in certain Cacteae. According to Mohl and De Bary, medullary bundles are only present in a few *Mammillarias* (e.g. *Mammillaria angularis*, but not in *M. pusilla*, *M. glochidiata* and others), in *Echinocactus*, in a few species of *Cereus* with thick shoots (e.g. *C. candicans?*), and according to Lauterbach also in *Echinopsis*; according to Vöchting, cortical bundles occur in species of *Rhipsalis*, *Lepismium* and *Pfeiffera*, and according to K. Schumann also in *Phyllocactus*. The cortical vascular bundles have a cambium, and thus grow in thickness like the bundles of the normal ring; they are essentially distinguished from the latter by the fact that prosenchymatous cells never occur in them. They form a dense network in the longitudinal direction, owing to numerous anastomoses.

A transverse section through the shoot of *Rhipsalis rhombea*, Pfr., shows a narrow band-shaped outline, the central portion being occupied by the normal vascular ring, while numerous cortical bundles, in groups of two or more, are found in the two wings. Almost all the Alatae in *Rhipsalis* (*R. crispata*, Pfr., *R. pachyptera*, Pfr., and *R. Swartziana*, Pfr., according to Vöchting) and the forms of *Lepismium*, characterized by their sharp angles, resemble *R. rhombea*; in the wings of all these plants the cortical vascular bundles lie in two rows, the bast-portions being directed towards the exterior. Amongst the Alatae, *Rhipsalis carnosa*, Vöcht. forms the sole exception, and only in so far as the cortical bundles occur not only in the wings, but also around the normal ring of bundles. When more than two wings are present, as is the case in many of the segments of the shoot in species of *Rhipsalis*, belonging to the sections Alatae and Angulosae (*R. paradoxa*, S. Dyck, *R. pentaptera*, Pfr., and *R. micrantha*, DC.), in some shoots of '*Lepismium, radicans*' and all shoots of *Lepismium Knightii* and *Pfeiffera cereiformis*, the position of the bundles remains the same as in shoots with two wings, except that the outline then becomes three-, four-, or many-angled. In these cases cortical bundles are sometimes (*R. paradoxa*), as in *R. carnosa* amongst the Alatae, also found in the portions alternating with the wings. *R. funalis* may serve as the type of the species of *Rhipsalis* belonging to the section Teretes (*R. floccosa*, S. Dyck, *R. funalis*, S. Dyck, *R. conferta*, S. Dyck, *R. Cassytha*, Gaertn., *R. pendula*, Vöcht., *R. Saglionis*, Otto, *R. mesembryanthoides*, Haw., *R. salicornoides*, Haw., *R. Lagenaria*, Vöcht.): the cortical bundles here lie in small groups, and form small rings of bundles among themselves.

The bundles of the normal vascular ring are concerned to a very varied extent in the formation of the axis. Beginning with *Pereskia*, in which the woody tissue of the vascular bundles forms the chief portion of the axis, all transitions are found to those species which possess weakly developed vascular bundles, and show an enormous development of the ground-tissue. In correspondence with the different degrees of development of the vascular bundles the composition of their xylem varies. In *Pereskia*, *Rhipsalis*, most species of *Cereus*, and some *Opuntias* the compact wood consists of (*a*) wood-fibres with thick walls and simple slit-shaped pits; according to H. Schenck, they

are occasionally septate in *Pereskia aculeata*, Plum.; (*b*) pitted vessels, which are sometimes accompanied by spirally thickened vessels in the middle of the secondary wood; (*c*) wood-parenchyma, which accompanies the vessels; and (*d*) lignified medullary rays. According to H. Schenck, the vessels attain a diameter of ·23 to ·25 mm. in *Pereskia aculeata*, Plum. (which is a high climber), and have simple perforations. According to Schleiden, the structure of the wood in most of the *Opuntias*, in *Echinocactus*, *Mammillaria* and *Melocactus* is quite different. In these cases elementary organs of quite a special nature (Fig. 91) occur in the wood; they are generally described as tracheides, but Van Tieghem, who demonstrated a protoplasmic sac and a nucleus in their contents, speaks of them as parenchymatous cells. They are broad cells with very thin walls, and in form are midway between the shape of a barrel and that of a spindle; they are provided with local annular or spiral thickening ridges, which are inserted on the thin wall by their narrow edge, and project far into the cell-lumen.

These cells seem to be entirely wanting in the species of *Pereskia* and *Rhipsalis*, and also in the stem of the species of *Cereus*. In the genus *Opuntia* they are also absent in some of the species, especially in all those which have flat oval shoots of the type of *Opuntia Ficus indica*, e.g. *Opuntia monacantha*, *O. brasiliensis*, *O. andicola*, &c. In other species of *Opuntia* they appear sparingly in the articulations between the segments, either in the tissue of the medullary rays lying between the bundles, or at the margin of the pith, and in no way enter into the vascular bundles themselves, e.g. in *Opuntia cylindrica*, *O. ramulifera*, and *O. andicola*; in other cases they themselves become an integral part of the vascular bundles, as in *Opuntia tunicata*, *O. imbricata*, &c. They are found in still larger quantities in *Echinocactus* and *Melocactus*, where—except in the lowest internodes—they already form the most important part of the xylem. Finally, in *Mammillaria simplex*, *M. rhodantha*, *M.* '*stelligera*,' &c., all other elements, with the exception of the tracheae of the primary xylem, disappear and the peculiar tracheides form the bulk of the xylem. Generally these tracheides are also distinguished from the actual vessels by lack of perforations. In *Echinocactus* and *Mammillaria*, however, rows of tracheides occur, in which the individual elements are connected by means of perforations.

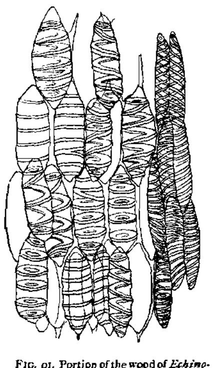


FIG. 91. Portion of the wood of *Echinocactus Eyriesii*.—After Schleiden.

The bast of the vascular bundles is strengthened by hard bast in certain members of the Order (species of *Pereskia*, *Rhipsalis*, *Cereus*, and *Phyllocactus*, according to Schleiden and Lauterbach). Similar groups of hard bast, arranged in a ring, are found in the primary cortex of *Lepismium sarmentosum*, Voecht. (Vöchting).

In the following paragraphs I shall speak firstly of the hairy covering, then of the thorns, and finally of the excretory and secretory structures. The **hairs** are (rarely) unicellular (*Echinocactus*, according to Michaelis), uniseriate, biseriate or multiseriate. According to Caspari, the multicellular trichomes are composed of cells which are short and narrow in the basal portion of the hair, whilst they are broader and longer towards its termination; the cells are sometimes provided with pits or with superficial striation Glandular hairs have not been observed in the Order. The extranuptial nectaries, which have been found by Delpino and others in some Cacteae (species of *Cereus*, *Mammillaria*, *Opuntia*, and *Rhipsalis*), have nothing to do with

epidermal structures, but are cushion-shaped bodies, arising in the same way as the thorns, which will be described immediately, and excreting a fluid containing sugar.

The structure of the **thorns** (Fig. 92), the determination of the morphological value of which has occupied a number of investigators, has been most thoroughly examined by Caspari. His observations extend to more than a hundred species of the genera *Mammillaria*, *Anhalonium*, *Melocactus*, *Echinocactus*, *Pilocereus*, *Echinopsis*, *Cereus*, *Rhipsalis*, *Lepismium*, *Pfeiffera*, *Pereskia*, and *Opuntia*. This is not the place for a detailed discussion of the reasons for regarding these structures as foliar organs. It must suffice to refer to the interpretation of Delbrouck, who regards the thorns of the Cacteae as a transition between 'leaf-prickles' (Phyllomstacheln) and 'trichome-prickles,' to the views of Caspari and K. Schumann, who consider the structures in question as being of the nature of emergences, and to the works of Zuccarini, Kauffmann, Goebel, Wetterwald, and Ganong, who support the theory of the foliar nature of the thorns.

Vascular bundles generally take no part in the formation of the thorns[1]. The latter consist of a bundle of sclerenchymatous cells with thick walls and devoid of pits, and immediately surrounded by pitted sclerenchyma-cells with relatively thin walls. The outer covering is composed of epidermal cells, which have wide lumina, and invariably show a different structure at the apex from that at the base of the thorn. This difference is most clearly marked in the thorns of all the species of *Opuntia* (with the single exception of '*Opuntia clavarioides cristata*,' which perhaps belongs to *Cereus*), and in the thorns of some *Pereskias* (viz. in the two species of the group Subcarnosae, Foerst.: i.e. *P. spathulata*, Link, and *P. subulata*, Mühlenpf., which should perhaps be united with *Opuntia*, but not in the species of the section Frutescentes, Foerst., with *P. aculeata*, Plum., *P. grandifolia*, Haw. and *P. Bleo*, DC.). In the *Opuntias* (see Fig. 92) and the two first-named species of *Pereskia* the integumental cells of the tip of the thorn are scaly; they are flat and lie in an imbricate manner over one another, whilst the apex of each cell is covered by the freely projecting end of the preceding cell, which is more or less distinctly produced into three points. The free ends of the scale-cells are directed backwards towards the base of the thorn, and serve as hooks. The structure of the thorns just described had previously been pointed out by Engelmann as highly characteristic of the genus *Opuntia*, and as forming a point of difference from the other members of the Order. In the latter a difference in the structure of the apex and base of the thorn is also noticeable, but is due to the fact that the cells of the apex are chiefly prosenchymatous, while those of the base are mainly parenchymatous. In addition to this the basal cells sometimes exhibit markings or prominences on their membrane (as in *Mammillaria*, *Echinocactus*, *Pilocereus*, *Cereus*, *Pfeiffera*, and *Rhipsalis*). According to Caspari, the last-mentioned features can only be employed in specific diagnosis.

FIG. 92. Thorn from the leaf-cushion of *Opuntia Ficus indica*, Mill.—Original.

As regards the structure of the thorns the following general statements may be added. Their epidermal cells invariably possess straight and never undulated lateral walls. They are arranged on the thorn in longitudinal rows with a spiral course (from right to left in the botanical sense). The

[1] The transitional forms between thorns and leaves, which Kauffmann first observed forty years ago (Bull. Soc. imp. de Nat. de Moscou, xxxiv, 1859) and which have more recently again been met with by Ganong, alone contain a vascular bundle in their basal portion.

angle of inclination of this spiral line with reference to the longitudinal axis of the thorn sometimes varies in the same thorn, and is therefore not of systematic importance. The coloration of the thorns is caused by the deposition of colouring-matter in the membrane or lumen of the inner sclerenchymatous cells. The calyptra of the prickles of some *Opuntias* (*O. tunicata*, Hort., Berol., &c.) consists of thick-walled cells, under the protection of which the cells of the thorn gradually undergo sclerosis.

The **excretory and secretory structures** of the Cacteae have been studied in special detail by Lauterbach. Of these the crystalline excretions of oxalate of lime are the most important, but laticiferous canals and mucilage-cells are also found, and a few other cases of rarer occurrence may be added. Before entering into details regarding these points we may prefix the synopsis given by Lauterbach of the occurrence and distribution of the various structures in question :

I. Crystal-cells alone are present : (*a*) irregularly distributed in : *Anhalonium*, *Mammillariae longimammae* (*M. longimamma*, DC.), *M. crinitae* (*M. Bocasana*, Poselg., *M. glochidiata*, Mart., *M. multiceps*, S. Dyck), *M. heteracanthae*, pro parte (*M. sanguinea*, Haage, *M. elegans*, DC., *M. Haageana*, Pfr., *M. rhodantha*, Link et Otto, *M. pulchella*, Hort. Berol., *M. fulvispina*, Haw.), *M. subsetosae* (*M. dolichocentra*, Lem.), *M. stelligerae* (*M. subechinata*, S. Dyck, *M. anguinea*, Otto, *M. rufocrocea*, S. Dyck, *M. elongata*, DC., *M. Stella-aurata*, Mart., *M. gracilis*, Pfr.), *Mammillaria elephantidens*, Lem., *Rhipsalis paradoxa*, S. Dyck ; (*b*) forming a connected layer beneath the epidermis, owing to a single solitary or clustered crystal occurring in each cell of the hypoderm : in *Pelecyphora*, *Astrophytum*, and *Echinocactus*, in most cases.

II. The following possess laticiferous canals and crystal-cells : *Mammillariae centrispinae* (*M. applanata*, Engelm.), *M. angulares* (*M. Webbiana*, Lem., *M. crocidata*, Lem., *M. Emundtsiana*, Hort., *M. Bockii*, Foerst., *M. viridis*, S. Dyck, *M. hystrix*, Mart., *M. Foersteri*, Mühlenpf., *M. pyrrhocephala*, Scheidw., *M. centricirrha*, Lem., *M. Hopferiana*, Linke, *M. glauca*, Dietr., *M. cirrhifera*, Mart., *M. angularis*, Link et Otto, *M. subangularis*, DC., *M. megacantha*, S. Dyck, *M. Neumanniana*, Lem., *M. Krameri*, Mühlenpf., *M. pentacantha*, Pfr., *M. magnimamma*, Haw., *M. gladiata*, Mart., *M. Zuccariniana*, Mart., *M. macracantha*, DC.), *Mammillaria nigra*, Ehrenb., *M. rhaphidacantha*, Lem., and *M. macromeris*, Engelm., also *Leuchtenbergia principis*, Fisch. (here the laticiferous canals have scanty contents).

III. Mucilage-cells and crystal-cells are present: (*a*) crystal-cells irregularly distributed : *Malacocarpus*, *Echinocactus Ottonis*, Lem., and *E. Monvillei*, Lem., *Echinopsis*, *Pilocereus*, *Cereus*, *Echinocereus*, *Phyllocactus*, *Epiphyllum*, *Rhipsalis*, *Pfeiffera*, *Lepismium*, and *Pereskia* ; (*b*) crystal-cells forming a connected layer beneath the epidermis: *Mammillaria macrothele*, Mart., *Melocactus*, *Opuntia*, *Pereskia subulata*, Mühlenpf.

The mucilage-cells are found in the whole of the ground-tissue ; their physiological importance as water-reservoirs is evident. The marginal portion of the mucilage exhibits stratification, running parallel to the cell-wall, whilst an irregularly shaped mass of mucilage usually occupies the middle of the cell. Sometimes crystals occur in the mucilage-cells. It has not yet been definitely determined whether the contents of the mucilage-cells are derived from the protoplasm (according to Lauterbach), or from the cell-membrane (according to De Bary and Walliczek), or from both (according to Longo ?).

In addition to the mucilage-cells lysigenous mucilage-canals occur in a number of species of *Opuntia* with the segments of their shoots flattened like leaves, such as *O. decumana*, Haw. ; these canals are situated externally to the bast of the more strongly developed vascular bundles (Schleiden, De Bary, and Longo [1]).

The laticiferous canals, as is apparent from the above conspectus, are found in many, but not in all species of ***Mammillaria***, as well as in *Leuchten-*

[1] Lauterbach curiously enough did not observe these canals, although he searched for them.

bergia principis[1]. They are to a certain extent characteristic of groups of species in *Mammillaria*. In this genus their contents consist of a thick whitish sap, which rapidly hardens on exposure to the air; these contents are insoluble in water, but soluble in chloroform after long exposure to this reagent, and also soluble in ether; they are stained bright red by tincture of alkanna, and may therefore be considered as a mixture of resin- and caoutchouc-like substances. The diameter of the canals is between ·042 and ·14 mm. With regard to the distribution of the laticiferous canals the following facts may be pointed out on the authority of Lauterbach. In the interior of the plant the canals are isolated, but they increase in abundance towards the periphery. In the cortical parenchyma they anastomose with one another, and send numerous branches into the superficial, chlorophyll-containing parenchyma, especially into that of the warts, where the canals extend to the region just beneath the hypoderm. In the cortical parenchyma of the roots we again meet with these canals (with a diameter = ·07–·14 mm.), but they do not appear to extend into the small lateral roots. Gutwinski in his paper points out the fact that the laticiferous canals of *Mammillaria* are never met with in the pith and medullary rays, and hence occur in the cortical parenchyma only. The mode of origin of the laticiferous canals is lysigenous, according to Gutwinski and Lauterbach.

Oxalate of lime is sometimes excreted in enormous quantities in this Order,

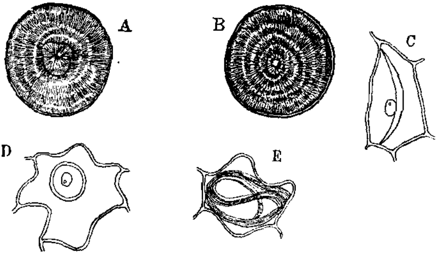


FIG. 93. A, B, Sphaerites of *Phyllocactus* sp.; C–E, Proteid-bodies of *Epiphyllum*; C, *E. Russelianum*, D–E, *E. truncatum*.—A, B after Kohl, C–E after Molisch.

so that it forms as much as 85 per cent. of the weight of the ash of the entire plant (in *Cephalocereus senilis*, according to Schleiden). Both solitary and clustered crystals occur, and the latter vary in shape. According to Lauterbach, the most widely distributed form is that of star-shaped clustered crystals, composed of monoclinic prisms; they are especially characteristic of the *Opuntias*. Almost as abundant as these are very irregular clustered crystals, likewise consisting of monoclinic prisms, which, however, have quite a short principal axis. Solitary crystals are rare in this Order; quadrate octahedra, tetragonal and monoclinic prisms are found. Bundles of raphides, composed of monoclinic prisms with a very long principal axis, have been observed by

[1] *Echinocactus Williamsii*, Lem. and *E. Lewinii*, Henn. also possess laticiferous canals according to K. Schumann, who describes the secretory elements in question as 'latex-sacs,' contrary to the customary nomenclature, and incorrectly ascribes a schizogenous mode of origin to them (see below); according to Michaelis, on the other hand, laticiferous canals are not found in these two species.

Lauterbach in *Opuntia Ficus indica* and *Echinocactus Ottonis*. According to Moebius and Kohl, very fine sphaero-crystals (Fig. 93, *A–B*) of oxalate of lime occur in some species. They have a spherical or ellipsoidal shape, their diameter varying between ·0125 and ·02 mm. Sometimes they resemble half-compound starch-grains, as they contain several centres, about which the outer layers are arranged. According to Kohl, it is doubtful whether these sphaerites are of systematic value for the species in which they occur. Nevertheless brief reference may be made to a few plants containing sphaero-crystals, and to the place of occurrence of the latter, on the basis of Kohl's observations, without however entering into the special structure of the sphaerites in the different species: thus sphaerites are found in the apices of the mammillae of *Mammillaria Wildiana* and *M. macrothele*, in the stem of *Epiphyllum* sp., *Cereus rostratus*, *C. nycticalus* and *Phyllocactus grandis*, and in the root of *Cereus rostratus*. Finally, the idioblasts of *Opuntia Lemaireana*, which contain clustered crystals and have been described by Kasimir, remain to be mentioned; they have very thin walls and on superficial observation might be taken for clustered crystals, lying in intercellular spaces. Crystals of oxalate of lime are excreted in the cell-wall of the epidermis and of the subepidermal cell-layer in *Pereskia Bleo*, according to the same author.

To complete the discussion of the cell-contents in the ground-tissue of the Cacteae, it remains to mention the frequent occurrence of sphaerocrystalline masses of undetermined nature, which Lauterbach and others have found deposited in alcohol material. It is also necessary to say a few words on the curiously-shaped proteid-bodies (Fig. 93, *C–E*) which were discovered by Molisch in the branches of *Epiphyllum*. In all species of this genus large proteid-bodies are found in every cell of numerous, island-like areas, which occur in the epidermis and the neighbouring cortical parenchyma. As a rule these bodies have the shape of a straight or bent spindle, a ring or a very long, thin thread, which is sometimes rolled up; the first two forms are commonly stratified to such an extent that they appear to be composed of threads, which are united by a substance of a different refractive index; the threads are found either singly or several in the same cell, and often attain considerable length. Molisch regards these structures as reserve-substances, Chmielewsky as secretions [1].

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[1] Similar bodies are found in the Orchid *Oncidium microchilum* (Mikosch, Ber. deutsch. bot. Gesellsch. 1890), in *Tecophilea cyanocrocus*, belonging to the Haemadoraceae (Wakker, in Pringsheim Jahrb., Bd. xxiii) and in the tentacles of *Drosera dichotoma* (Gardiner).

Tab. ii, iii.—Kohl, Kalks. u. Kiesels., 1889, p. 32.—Van Breda de Haan, Anat. van het geslacht *Melocactus*, Haarlem, 1891, 123 pp. and 3 Tab.—Benecke, Nebenz. d. Spaltöffn., Bot. Zeit. 1892, pp. 586-8.—H. Schenck, Anat. d. Lianen, 1893, p. 148.—Schumann, in Natürl. Pflanzenfam., iii. Teil, Abt. 6a, 1894, p. 164 et seq.—Walliczek, Membranschleim, Pringsheim Jahrb., Bd. xxiii, 1893, p. 262 et seq.—Ganong, Morph. u. Biol. d. C., Diss., München, and Flora 1894, Ergänzungsband.—Kasimir, Cristaux chez *Opuntia* et *Pereskia*, Bull. Herbier Boissier, t. ii, 1894, pp. 499-500.—[Longo, Mucilagine delle Cactee, Bull. della Soc. bot. Ital. 1896, pp. 50-2.]—Michaelis, Vergl. Anat. d. Gatt. *Echinocactus*, *Mammillaria* u. *Anhalonium* etc., Diss., Erlangen and Halle a. d. S., 1896, 39 pp. and 3 Tab.—Longo, Idioblasti muciferi delle C., Annuar. R. Ist. bot. di Roma, vol. vii, 1897, 14 pp. and 1 Tab., and Intorno ai canali delle Opunzie, loc. cit., 6 pp. and 1 Tab.

FICOIDEAE.

1. Review of the Anatomical Features. According to the existing investigations the following features in the structure of the axis may be regarded as characteristic: the anomalous stem-structure, the lack of parenchymatous medullary rays, the simple pitting of the prosenchymatous ground-tissue, and of the wood-prosenchyma, and the simple perforations of the vessels. The anomalous structure of the axis is, however, only present in the species with thick stems (exception: *Polpoda*); in these the transverse section of the axis either shows several concentric rings of vascular bundles (*Tetragonia*-type) or bundles, which may be concentrically or irregularly arranged, embedded in a prosenchymatous or partly parenchymatous ground-tissue (*Mesembryanthemum*-type). Cork-formation is (at least in *Mesembryanthemum*) internal. In the leaf-structure, the occurrence of large, water-storing, bladder-like cells in the epidermis (Fig. 94, *A–B*) and of aqueous tissue in the interior of the leaf in many species may be especially pointed out. A constant and characteristic type of stoma is not found; in some of the species of *Mesembryanthemum*, however, subsidiary cells are present, which are placed parallel to the pore. With the exception of very large tannin-sacs occurring in the leaf-tissue of some species of *Mesembryanthemum*, internal secretory organs are wanting. The hairy covering consists of simple unicellular hairs, unicellular two-armed trichomes (*Aizoon*, *Galenia*, and *Plinthus*), and stellate hairs with a uniseriate stalk and a terminal cell, assuming the form of a star (*Glinus* and *Mollugo* respectively, Fig. 94, *C*). Oxalate of lime is excreted in the form of raphides (*Mesembryanthemum* and *Gisekia*), styloids (axis of *Aizoon* and *Tetragonia*) and clustered crystals; in *Mesembryanthemum* it also occurs as a deposition in the cell-wall in the form of small crystalline granules, found principally in the outer wall of the epidermal cells of the leaf.

2. Structure of the Leaf. Only a relatively small number of species has been investigated with regard to their leaf-structure, which shows a distinct adaptation to the dry desert-regions where the members of this Order occur. The highly characteristic epidermal differentiation (Fig. 94, *A–B*), which is often found on the stem as well, has been specially pointed out in many members of the Order by the various observers (Schrank, Mirbel, De Candolle, Meyen, Martinet, and later by De Bary, Hagen, Dannemann, Heinricher, and Volkens). Large, bladder-like **epidermal cells**, sometimes reaching the size of peas, are found intercalated among the cells of ordinary dimensions. The former must be regarded from a physiological point of view as water-reservoirs. When completely filled with water they give a peculiar appearance to the plants of this Order, to which the latter owe the name of ice-plants. Some of these large cells occasionally tend to form hairs; e.g. in *Tetragonia expansa*, where the bladder-like cells are attenuated in a papillose manner at the apex, and in *Mesembryanthemum crystallinum*, L. (Fig. 94, *A*), in which the bladders on the upper side of the leaf suddenly narrow down at the apex into a short and slender hair-like structure. In addition to the two

genera *Tetragonia* and *Mesembryanthemum*, these large bladder-cells are also found in various degrees of development in species of the genera *Aizoon* (e.g. *A. canariense*, L., Fig. 94 *B*), *Galenia* (e.g. *G. glauca*, Walp.), *Sesuvium* (e.g. *S. Portulacastrum*, L.), *Trianthema* (e.g. *T. crystallina*, Vahl), and *Telephium* (*T. sphaerospermum*, Boiss.). In the stomatal apparatus, according to Benecke and C. Schulze, special subsidiary cells are either wanting (*Mesembryanthemum crystallinum*, *Tetragonia expansa*; also in *Adenogramma*, *Gisekia*, *Limeum*, *Polpoda* and *Psammotropha*) or, when present, are situated parallel to the pore (*M. adscendens* and *M. uncinatum*). In the second case the stomata, moreover, lie more or less parallel to one another and transversely to the longitudinal axis of the leaf. The **structure of the leaf**, as far as it has been investigated, is centric. The entire mesophyll may consist of palisade-tissue, or the latter may form a subepidermal envelope surrounding a centrally situated, aqueous tissue, which is composed of large cells and encloses

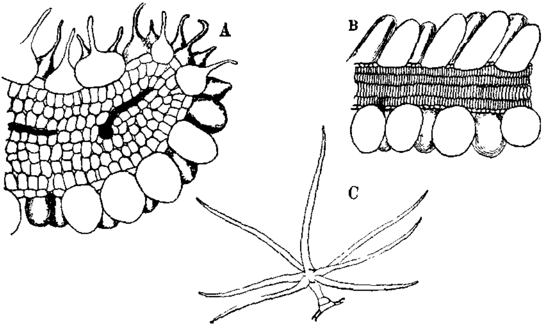

FIG. 94. A, Transverse section through the margin of the leaf of *Mesembryanthemum crystallinum*, L. B, Transverse section through the leaf of *Aizoon canariense*, L. C, Stellate hair of *Glinus Cambessedesii*, Fenzl. —A, B after Volkens, C Original.

the vascular system[1]. In some members of the Order (species of *Mesembryanthemum*, according to Pax) a covering of wax is present on the vegetative organs in order to diminish transpiration, in others a **hairy covering** serves the same purpose. This latter consists of simple unicellular hairs (*Mesembryanthemum Ecklonis* and *M. stelligerum*, according to Dannemann), unicellular two-armed hairs (species of the very closely related genera *Aizoon*, *Galenia* and *Plinthus*) and stellate hairs with a unicellular star (species of *Glinus*). The two-armed hairs vary in the thickness of their walls and in their appearance. In *Aizoon glinoides*, L. f., I observed relatively short trichomes with thin walls and equal arms, as well as very long hairs with thick walls and very unequal arms; in *Galenia secunda*, Sond. the two-armed hairs have thin walls, wide lumina, and equal arms. The stellate hairs of *Glinus Cambessedesii*, Fenzl (Fig. 94, *C*), possess a uniseriate stalk, formed of 2–4 cells and bearing a terminal cell, which is differentiated in the form of a star. Internal **secretory organs** are rare. In a few species of *Mesembryanthemum* only (*M. glaucum*,

[1] The anatomy of the biologically interesting forms, such as *Mesembryanthemum truncatellum*, Haw. and other species of the section *Sphaeroidea*, in which the opposite leaves are fused to form a hemispherical body, provided with an opening at the apex, has not yet been investigated.

&c.) tannin-sacs of large size are present, situated at a depth of one or two cell-layers beneath the epidermis of the leaf (Dannemann and Höhnel). **Oxalate of lime** is found in the leaf in the form of raphides (in the genera *Mesembryanthemum* and *Gisekia*), clustered crystals (in *Semonvillea* and *Limeum*, according to Blenk) or quite small crystalline bodies (*Psammotropha*, according to C. Schulze). In connexion with the occurrence of oxalate of lime we may briefly mention the deposition of small crystals of the same substance in the membranes of the epidermal cells of the leaf in species of *Mesembryanthemum*; this feature was first observed by Solms-Laubach. It gives the leaves a characteristic, chalky-white appearance. If the deposition is confined to circumscribed areas on the epidermis, they become noticeable as white spots. This deposition of oxalate of lime is essentially confined to the outer wall of the epidermis; it is entirely wanting or only takes place to a slight extent (the latter in *M. lacerum* and *M. stramineum*) in the inner and lateral walls. In the outer wall the entire cellulose portion is filled by the crystalline granules, except for a narrow lamella bordering on the cell-lumen. These granules are most densely crowded in *Mesembryanthemum Lehmanni*, where the lamella of the wall in which they occur appears in consequence to be almost homogeneously calcified; the same may be said of *M. lacerum*. The granules of calcium oxalate have a rounded shape, which is flattened in the direction of the invisible stratification of the cell-wall, the flattening being greater in proportion as the granules are more closely placed. Finally we may mention the occurrence of sphaero-crystals in alcohol-material of species of *Mesembryanthemum*; this was first observed by Kolderup-Rosenvinge. According to Hansen, they are invariably soluble in water and produce needles of gypsum when treated with concentrated sulphuric acid, which indicates that they contain lime.

3. STRUCTURE OF THE AXIS. The axis of the woody species is characterized by **anomalous structure**. Régnault has the merit of being the first to draw attention to this feature. The anomaly is the same as occurs in the Amarantaceae and related Orders. Rings or arcs of meristem appear successively in the pericycle of the stem, giving rise to secondary vascular bundles and intermediate tissue (Morot).

According to the structure of the intermediate tissue and the arrangement of the vascular bundles two types of transverse section may be distinguished. The first (*Mesembryanthemum*-type) shows a prosenchymatous ground-mass, in which numerous vascular bundles are embedded, arranged in more or less distinct concentric rings. To this type belong: *Mesembryanthemum crystallinum*, *M. multiflorum*, and *M. tuberosum*, according to Régnault, *M. bulbosum*, Haw., *M. echinatum*, Ait., *M. filicaule*, Haw., *M. floribundum*, Haw., *M. Lehmanni*, Eckl. et Zeyh., *M. lupinum*, Haw., *M. rubricaule*, Haw., *M. spectabile*, Haw., and *M. umbellatum*, L., according to Falkenberg, *M. geminiflorum*, according to Dannemann, *M. bracteatum*, Ait. and *M. gracile*, Haw. (see my 'Holzstruktur'); further, *Galenia africana*, *Tetragonella* '*amplexicaulis*'[1] and *Trianthema pentandra*, according to Régnault, as well as *Acrosanthes teretifolia*, Eckl. et Zeyh. (see my 'Holzstruktur'), and *Sesuvium congense*, Welw., according to Pax. The second type (*Tetragonia*-type) consists in the alternation of more or less complete rings of xylem and phloem in the transverse section of the stem, i. e. secondary vascular rings are present. This second type has been met with by Régnault and me in *Aizoon elongatum*, Eckl. et Zeyh., and *A. propinquum*, Eckl. et Zeyh., *Glinus lotoides*, L., *Sesuvium Portulacastrum*, *Tetragonia crystallina*, *T. expansa*, *T. fruticosa*, L., and *T. spicata*, L. f. Pax provisionally includes the genera *Glinus*, *Aizoon*, *Trianthema*, *Tetragonia*, *Orygia*, *Pharnaceum*, and *Macarthuria* in this type. Between the two types, however, transitions occur. The phloem-portions of the secondary vascular bundles are not always rounded in the first type, especially in species of *Mesembryanthemum*, but are sometimes elongated in the tangential direction in the form of bands, so that a transition to the second

[1] Annon sphalmate ex '*amplexiroma*'?

type is indicated, notably when the bundles show a well-marked concentric arrangement. On the other hand, in *Aizoon propinquum*, for example, which belongs to the second type, the phloem-rings are found to be locally interrupted by groups of prosenchymatous cells uniting the rings of wood in a radial direction; in this way there is a certain approximation to the appearance of the transverse section in the first type.

According to C. Schulze, the herbaceous genera *Adenogramma*, *Gisekia*, *Limeum*, and *Psammotropha*, as well as the woody genus *Polpoda*, differ from most of the woody species in possessing **normal structure**. Some of the genera named, however, are referred to other Orders (Portulaceae, Phytolaccaceae, &c.) by certain systematists.

The following points may be mentioned with regard to the structure of the **xylem**. Ray-parenchyma of the normal (parenchymatous) type is wanting in both groups of species. The spiral tracheae of the primary xylem are only found in the innermost bundles (the leaf-trace bundles). The prosenchyma always bears simple pits, whether it constitutes part of the ground-tissue or is actual wood-prosenchyma, i.e. such as belongs to the vascular bundles. According to the statements of Falkenberg and Morot, unlignified parenchyma may, however, take part in the formation of the ground-tissue in *Mesembryanthemum* to a variable extent. Thus in *M. Lehmanni*, Eckl. et Zeyh. abundant parenchyma appears side by side with the prevalent prosenchyma; in *M. lupinum*, Haw. the prosenchymatous cells are entirely wanting, and the ground-tissue consists solely of thin-walled parenchyma. The vessels have walls with bordered pits and simple, circular or elliptical perforations. I have observed delicate spiral thickening of the vessel-wall in *Galenia africana*, and delicate striation in *Tetragonia fruticosa*.

Our detailed knowledge of the structure of the **cortex** is confined to the genus *Mesembryanthemum*. The bladder-like water-storing cells are also found in the epidermis of the stem. The outer cortical tissue is sometimes differentiated as more or less typical assimilatory tissue. Some species (*M. crystallinum*, *M. imbricatum*, *M. splendens*, &c.) possess cortical bundles[1]; these consist of thin branches of the petiolar bundles, passing into the stem at the nodes and dividing into small ramifications, which anastomose in a reticulate manner, and penetrate downwards into the cortex without reaching the next node below. In other species (*M. Haworthii*, *M. rigidicaule*, *M. umbellatum*) a zone of collenchymatously thickened cells is present on the outer side of the ring of meristem. According to Dannemann, periderm-formation is internal; the phellogen develops from one of the innermost cell-layers of the cortex (*M. splendens*), or the outermost cell-layer of the collenchymatous zone just mentioned (*M. rigidicaule*), or the outermost cell-layer of the meristematic ring.

Oxalate of Lime has been observed (*a*) in the ground-tissue of the axis of *Mesembryanthemum* in the form of raphides, which are sometimes contained in suberized sacs (Höhnel, Zacharias), (*b*) in the soft bast of *Aizoon propinquum* in the form of styloids, (*c*) in the pith of *Tetragonia spicata* in the form of styloid-like crystals, and (*d*) in the cortex of *Tetragonia expansa* (Régnault) and *Limeum* (C. Schulze) in the form of clustered crystals.

4. STRUCTURE OF THE ROOT. The **anomalous structure** of the stem is generally repeated in the root (*Mesembryanthemum*; *Tetragonia expansa*, according to Lohrer and Morot; *Aizoon hispanicum*, according to Morot; *Mollugo radiata*, Ruiz. et Pav., according to my own observation). On the other hand, I have observed the wood of the root to have normal structure in *Pharnaceum incanum*, L. and *Psammotropha quadrangularis*, Fenzl.

[1] Russow's statement regarding the occurrence of medullary vascular bundles with concentric structure in *M. crystallinum* is incorrect.

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UMBELLIFERAE.

1. Review of the Anatomical Features. Like the closely related Araliaceae the members of this Order are distinguished by the possession of schizogenous resin-canals, which moreover occur in the same position as in the former Order. The following are further anatomical features, found in most or all of the Umbelliferae: the presence of collenchymatous strands in the primary cortex, corresponding to the ribs of the stem; the ultimate disappearance of the pith in the internodes; and the fact that the fibro-vascular strands of the petiole are invariably isolated. The type of stoma is not uniform. The perforations of the vessels are chiefly simple; the wood-prosenchyma of the woody species is provided with simple pits, either wholly or partially. The development of cork usually takes place superficially. With regard to the hairy covering, it should be noted that glandular hairs have not been observed but that simple unicellular hairs occur occasionally, and also multiseriate shaggy hairs (*Hydrocotyle*), abietiform hairs (*Xanthosia*, Fig. 95, *A–B*), and stellate hairs (*Bowlesia*, Fig. 95, *C*). Oxalate of lime is principally found in the form of clustered crystals, but in the axis it also appears in the form of solitary crystals. The following anatomical features, which can only be employed in specific diagnosis, are especially noteworthy: the appearance of medullary bundles in the stem with varied orientation (see also Fig. 96); the very variable appearance of the transverse section of the petiole; the occurrence of cortical groups of vascular bundles in certain *Eryngia* having a monocotyledonous habit; the appearance of an extrafascicular ring of growth in the rhizome of *Eryngium Lassauxii*, Decne. and *E. Serra*, Cham. et Schlecht.; the secondary transformation of the vascular system of the root into concentric vascular bundles (Fig. 97) in certain species of *Oenanthe*, &c.

2. Structure of the Leaf. Numerous investigations of the structure of leaf and axis in this Order exist in the literature; these, however, always take only a small number of the genera and species of this large Order into consideration, while special attention is paid to one or other of the anatomical features. As a consequence it is not feasible to enter into all the detailed statements of the authors in the following sections, the object of which is to give an exact review of the anatomical features appearing in the leaf and axis of the Umbelliferae.

The **leaf-structure**, as might be expected, varies. It is mostly bifacial, but it is centric in those leaves which only have very narrow or terete segments, as for example in *Foeniculum officinale*, All. and in the leaves of *Bupleurum*. The **stomata** may occur on both sides of the leaf or only on the lower side. In the species of *Eryngium* with a monocotyledonous habit they are arranged parallel to one another, as in the Monocotyledons, and are accompanied by subsidiary cells, parallel to the pore (Moebius). Subsidiary cells of the latter type also occur in *Xanthosia hirsuta*, DC., according to my own observation, while in *Hydrocotyle Chamaemorus*, Cham. et Schlecht. all transitions from the Rubiaceous to the Acanthaceous type are found, viz. subsidiary cells, which are placed parallel, as well as transversely or obliquely to the pore; in the representatives of the other tribes which I have examined (*Ammi Visnaga*, Lam., *Bowlesia tropaeolifolia*, Gill. et Hook., *Caucalis daucoides*, L., *Laserpitium latifolium*, L., *Mulinum cuneatum*, Hook. et Arn., *Peucedanum alsaticum*, L., *Prangos uloptera*, DC., *Sanicula europaea*, L. and *Seseli petraeum*, Bieberst.) the stomata are surrounded by several neighbouring cells of the ordinary kind, sometimes three in number (*Sanicula*, *Peucedanum*). According to Volkens, the stomata on the stem of *Deverra triradiata*, Hochst. and *D. tortuosa*, DC. lie in basin-shaped depressions, which, in the same way as in certain Coniferae, are filled with a resinous or wax-like mass. Hypoderm has been observed in the leaf in *Bupleurum graminifolium* (one-layered) by Klausch, in *Aciphylla carnosula*, F. von Müll. (one-layered beneath the entire epidermis) and *Eryngium vesiculosum*, Labill. ('three-layered epidermis') by Diels, and in the *Eryngiums* with a monocotyledonous habit (on both sides, as in *E. paniculatum*, Cav., or only on the lower side) by Möbius and Pfitzer.

With regard to the general leaf-structure, *Foeniculum officinale* and the species of *Eryngium* with a monocotyledonous habit may be discussed in somewhat greater detail. The circular transverse section of the leaf of the first-named plant exhibits beneath the epidermis an envelope of palisade-tissue, locally interrupted by bundles of collenchyma; in the interior of the leaf, vascular bundles, arranged in a ring, correspond in position to the bundles of collenchyma. In the species of *Eryngium* having a monocotyledonous habit, the leaves, which are provided with parallel veins, are in some cases traversed by air-canals in the longitudinal direction, parallel to the veins; these air-canals are interrupted by diaphragms at certain intervals. In the longitudinal septa, separating the air-canals from one another, run the vascular bundles of the veins; these bundles are mostly in twos, of which the upper one is inversely orientated. In the lamina the upper and lower sides of the leaf exhibit almost identical structure, except that in many species the sclerotic hypoderm is confined to the lower side, although in other cases it occurs on both sides of the leaf. Beneath the epidermis or the hypoderm, as the case may be, broad strips of palisade-parenchyma and narrower bands of fibre-like sclerenchyma alternate on both sides of the leaf; the sclerenchyma-strands are found above and below the vascular bundles of the veins, and also between them, although they are less strongly developed in the latter position. Regarding the structure of the septate leaves of species of *Ottoa*, *Crantzia*, and *Tiedmannia*, see Briquet.

As general features in the structure of the **petiole** it may be mentioned that the vascular bundles invariably have an isolated course and that, as in the stem, subepidermal collenchymatous strands are mostly to be found opposite the peripheral vascular bundles. The bundles of the petiole are either arranged in a ring or in an arc; medullary bundles are not uncommon, and vary in number. All those species which possess medullary vascular bundles in the stem also exhibit them in the petiole. The converse of this statement is, however, not correct; for in many species which have no medullary bundles in the stem, such bundles are found in the petiole. Their occurrence in the petiole, as in the stem, is only a specific peculiarity. The medullary vascular bundles are, as a rule,

simply collateral; but by the fusion of the contiguous xylem-portions of two bundles apparent bicollateral bundles originate, whilst secondary development of woody tissue on the bast-side of the originally simple collateral bundles, results in more or less completely concentric structure with central phloem.

Oxalate of lime is found in the leaf, principally in the form of clustered crystals; in many cases it is entirely absent. In the bast of *Xanthosia hirsuta* solitary crystals are also present.

With regard to the **hairy covering**, it may be mentioned that glandular hairs have not been observed; species of *Siebera* are, however, described by Bentham and Hooker as 'frutices . . . tenuissime glanduloso-puberuli,' a point which requires further investigation[1]. Simple, unicellular hairs occur, for example, in *Caucalis daucoides*, as also in *Torilis Anthriscus*, Gmel., in which the wall of the hair is thickened in a verrucose manner and

FIG. 95. Trichomes of some Umbelliferae: A, B, *Xanthosia pilosa*, Rudge; C, *Bowlesia tropaeolifolia*, Gill. et Hook.—Original.

calcified; the leaf of *Prangos uloptera* bears short unicellular bladder-like trichomes; *Xanthosia pilosa*, Rudge, has hairs consisting of a number of tiers and resembling a fir-tree, these hairs being composed of a few short basal cells with thin, yellow walls, whilst the ray-cells in the tiers are pointed and have thick walls and narrow lumina (Fig. 95, *A–B*); *Bowlesia tropaeolifolia*, Gill. et Hook. has stellate hairs, provided with a biseriate or multiseriate pedestal, and four or more ray-cells, which are spread out in one plane on the lower side of the leaf (Fig. 95, *C*), whilst they are directed upwards on the upper side of the leaf; *Hydrocotyle Chamaemorus* has long, conical, multiseriate shaggy hairs, rounded off at the end[2].

The **resin-canals** of the Umbelliferae may now be discussed; they occur in all the vegetative parts of the plant, and sometimes exhibit a characteristic

[1] Elsewhere the leaf-teeth sometimes function as mucilaginous secretory organs on the young leaves of the Umbelliferae (see Reinke, loc. cit.).

[2] Drude also mentions 'pili glochidiati' in the genus *Drusa*.

arrangement, which is, however, probably in all cases only of value for specific diagnosis. In the stem, resin-canals have been observed in the primary cortex, pericycle (Van Tieghem) and pith, and sometimes also in the secondary bast. In the primary cortex they either occur subepidermally or in the middle of the strands of collenchyma or on the inner side of the grooved collenchyma-strands, or between the bast and the strands of collenchyma. In the secondary bast the resin-canals have been met with in woody species (*Heteromorpha arborescens*, Cham. et Schlecht., and *Bupleurum fruticosum*, L.) and in the 'Rhizoma Imperatoriae.' In the pith the resin-canals are found in most members of the Order (exceptions: *Bupleurum Gerardi* and *B. ranunculoides*, according to Trécul, and *Hydrocotyle vulgaris* and *Xanthosia rotundifolia*, according to De Bary); they occur in the interior of the pith, especially when the latter is persistent. In the numerous species with fistular internodes, the medullary resin-canals are mostly confined to the persistent peripheral part of the pith. In a few cases only, the canals are present in the middle of stems which become fistular; in these cases they are either isolated and lie free in the cavity, ensheathed by a few layers of pith-cells (*Smyrnium Olusatrum*), or they are embedded in persistent lamellae of pith, which project into the cavity from the periphery (*Heracleum Sphondylium*). In the internodes of the stem the resin-canals have rather a straight course, and scarcely branch or anastomose; in the nodes, on the other hand, numerous anastomoses and branches are found. Blind terminations of the resin-canals have not been observed in the stem; the secretory sacs, described as occurring in the older rhizomes of *Imperatoria*, are merely immense, bladder-like, local enlargements of the resin-canals[1]. In the petiole the resin-canals exhibit a similar distribution to that found in the stem; thus they lie in those portions of the ground-tissue which correspond to the pith, external cortex and pericycle, and, as K. Müller has shown in the case of a number of species, they also occur in the bast. The branches of the resin-canals also enter into the lamina of the leaf, where they accompany the vascular bundles of the veins into the branches of the third or even of the fourth order; they occur on both the upper and lower side of the bundles, their number varying from one to several, according to the thickness of the vein; finally their terminal branches anastomose to form a network. In the primary tissues of the root the resin-canals are confined to the periphery of the vascular strand (the pericambium), immediately internal to the endodermis. They are here found opposite the xylem as well as the phloem-groups of the vascular strand, just as in the roots of the Pittosporaceae and Araliaceae. The result is the same in both cases, leading to an anomalous origin of the lateral roots, which arise between the two resin-canals, placed opposite a xylem- and a phloem-group respectively, so that they are twice as numerous as the xylem- or phloem-groups, which together form the fibro-vascular system of the root (Van Tieghem). In the older roots of Umbelliferae the resin-canals are found in the secondary bast, sometimes (e.g. in *Myrrhis odorata* and *Opopanax Chironium*, according to Trécul and Van Tieghem) also in the wood. The contents of the resin-canals, briefly described, consist of ethereal oils, together with resin, or of milky mixtures of these substances with mucilage and solutions of gum; in the fresh state they may be either clear or turbid, and vary from milky-white to yellow in colour.

3. STRUCTURE OF THE AXIS. The stems in most members of the Order are ribbed. The ribs correspond to strands of collenchyma in the outer cortex, which are either immediately subepidermal or lie 2 or 3 cell-layers internal to the epidermis. Sometimes a ring of collenchyma is found in place of the isolated collenchymatous strands, as for example in *Bubon Galbanum* and

[1] Similar enlargements are mentioned by Dutailly in the cortex of the root of *Pastinaca sativa*.

in many *Eryngiums*, or the collenchyma is replaced by strands of sclerenchymatous fibres, as in the axis of the inflorescence of *Eryngium aquaticum*, L. (according to Möbius) or in the stem of *Chaerophyllum bulbosum* (according to De Bary). The collenchyma is rarely entirely wanting or very slightly developed (*Hydrocotyle vulgaris, Dimetopia, Mulinum*). Between the collenchyma-strands and throughout the outer portion of the primary cortex assimilatory parenchyma is found, and the cells of this tissue sometimes have a palisade-like shape (e.g. between the collenchymatous ribs of *Eryngium aquaticum* and in *Pimpinella Tragium*). The inner portion of the primary cortex consists more commonly of colourless parenchyma. The following special features in the anatomical structure of the outer cortex should also be mentioned here: the occurrence of a sclerosed epidermis in some species of *Bupleurum*, such as *B. Gerardi*, &c., and of a one-layered sclerosed hypoderm in the stem and in the axis of the inflorescence in species of *Eryngium*; the appearance of lacunae in the primary cortex of the stem in species of *Oenanthe*, in *Hydrocotyle vulgaris*, and in the axis of the inflorescence of *Eryngium aquaticum* (here of especially large size and corresponding in position to the furrows of the stem); the differentiation of the inner portion of the primary cortex of *Mulinum spinosum*, Pers. as a strengthening-ring, composed of elongated, lignified, fibre-like cells with wide lumina and slit-shaped pits, these cells passing over into typical fibre-like sclerenchyma towards the interior of the stem. The cork is developed subepidermally in *Bupleurum fruticosum* and *Heteromorpha arborescens*, according to my own investigation, and in species of *Hydrocotyle* and *Trachymene*, according to Noenen; on the other hand it originates in the pericycle in *Mulinum spinosum*[1].

With regard to the **fibro-vascular system** the most important point is the fact that most members of the Order possess a normal ring of vascular bundles, although medullary bundles commonly occur in addition. The vascular bundles are more rarely irregularly arranged in transverse section (*Ferula seseloides*, C. A. Mey., according to Drude). The ring of vascular bundles shows very varied differentiation[2], especially in the herbaceous species. The bundles often vary in size. In some cases they are isolated and separated from one another by ground-tissue. In other instances all or some of the xylem-portions of the vascular bundles are fused with one another by means of interfascicular libriform tissue. In a third series of cases the entire vascular bundles or only their outer (wood- and bast-) portions are embedded in a fibrous sheath, which is formed by interfascicular and pericyclic sclerenchyma. Pericyclic hard bast is also not rare in the other cases mentioned, and is developed to a varied extent. The xylem-ring of the woody species (such as *Xanthosia hirsuta*, DC., *Heteromorpha arborescens*, Cham. et Schlecht. and *Bupleurum fruticosum*, L.) is formed by vessels, wood-prosenchyma and narrow, uniseriate or biseriate secondary medullary rays. The vessels in the species named mostly have simple perforations; in *Xanthosia hirsuta* scalariform perforations with few bars are found as well. Scalariform perforations have also been met with accompanying the simple perforations in species of *Aethusa, Bupleurum, Carum, Hydrocotyle, Oenanthe* and *Peucedanum* by Noenen. In contact with parenchyma of the medullary rays the vessels bear simple (*Heteromorpha*) or bordered pits (*Xanthosia, Bupleurum*). In the herbaceous species and in rhizomes the walls of the vessels are commonly occupied by simple pits only. The wood-prosenchyma has simple pits; *Xanthosia* and other genera possess prosenchyma with bordered pits as well. The above-mentioned **medullary**

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[1] The incorrect statement made by Noenen that a two-layered endodermis occurs in a plant described as *Mulinum ferosa* (for *Mulinum Fragosa*?), is probably to be traced to the commencement of a development of corky tissue in the pericycle.

[2] For details see Drude, Noenen, etc.

vascular bundles have been met with in the stem of a number of Umbelliferae, but only constitute a specific peculiarity.

The species in which the various observers (Jochmann, Reichardt, Möbius, Courchet, Géneau de Lamarlière, Noenen, Drude) have found medullary vascular bundles are as follows: *Cachrys crispa*, Pers. and *C. laevigata*, Lam.; *Cenolophium Fischeri*, Koch; *Crithmum maritimum*, L.; *Eryngium Lassauxii*, Decne. (Rhiz.); *Ferula campestris*, *F. communis*, L., *F. Ferulago*, L., *F. glauca*, L., *F. granatensis*, *F. nudicaulis*, Spreng., and *F. seseloides*, C. A. Mey.; *Laserpitium alpinum*, *L. asperum*, Crtz., *L. latifolium*, L., *L. Nestleri*, S. W., and *L. Siler*, L.; *Oenanthe anomala*, Dur. et Coss., *O. crocata*, L., *O. globulosa*, and *O. pimpinelloides*, L.; *Opopanax Chironium*, Koch; *Peucedanum heterophyllum*, Vis., *P. officinale*, *P. Oreoselinum*, Mch., and *P. parisiense*, DC.; *Pimpinella Anisum*; *Silaus pratensis*, Bess.; *Sium latifolium*, L.; *Thapsia villosa*, L. The number, arrangement, and differentiation of the medullary vascular bundles vary greatly. Their number, for example, amounts to as much as 100 in *Ferula communis* (Reichardt), but is reduced to one in *Cenolophium Fischeri* or *Laserpitium alpinum* (Noenen). In a transverse section the medullary vascular bundles either exhibit an irregularly scattered arrangement (for details see Noenen) which may be confined to them (e.g. in *Laserpitium latifolium*) or may also extend to the peripheral bundles (e. g. in *Ferula seseloides*), or the greater number of the medullary bundles forms an inner ring, the bundles of which may be normally (e.g. in *Silaus pratensis*) or inversely (e.g. in species of *Oenanthe*) orientated with regard to the position of wood and bast; in the second case additional medullary bundles frequently occur in the interior of the pith or between the rings. In *Sium latifolium* the arrangement is especially noteworthy, for here the xylem-portions of the inner, inversely orientated, medullary ring of bundles are fused with the xylem-portions of the normal peripheral ring (Géneau de Lamarlière). The appearance of the transverse section of *Oenanthe crocata* (Fig. 96), *O. globulosa*, and *O. pimpinelloides* should also be noted; here three medullary vascular bundles occasionally replace a single one and correspond to each of the larger bundles of the peripheral ring, the xylem-portions of the medullary bundles being directed towards that of the peripheral bundle, and the four together forming a cross. Those medullary vascular bundles which are arranged in a ring have collateral structure, as may be gathered from what has already been said; those which are irregularly arranged, commonly have concentric structure (with central phloem) or apparently bicollateral structure (by fusion of the contiguous xylem-portions of two bundles) like the medullary vascular bundles of the petiole. With respect to the nature of the medullary bundles it may be remarked that, according to investigations by J. E. Weiss on *Silaus pratensis*, and contrary to the older statements of Jochmann and Reichardt, all these bundles ought probably to be regarded not as cauline but as continuations of vascular bundles of the peripheral ring in higher internodes.)

In addition to the medullary vascular bundles two other **anomalous structural features** of the stem have been observed in this Order, viz. cortical vascular bundles and the appearance of an extrafascicular vascular ring. According to Möbius, the cortical bundles are found in the axis of the inflorescence in some species of *Eryngium* with a Monocotyledonous habit, such as *E. Decaisneanum*, Urb., *E. paniculatum*, Delar., and *E. Serra*, Schlecht., and according to Noenen in *Siler trilobum* and in *Mulinum*. In the species of *Eryngium* the cortical bundles form a contracted vascular system, which originates by the fusion of several vascular bundles, arranged in a ring; they thus to some extent recall the well-known anomalous structures in certain Sapindaceous stems. The development of an extrafascicular cambial ring has been observed by Möbius in *Eryngium Lassauxii*, Decne. and *E. Serra*, Cham. et Schlecht.; externally it produces bast-like tissue, internally xylem with vessels.

With regard to the **pith** it may once more be pointed out that in most members of the Order this tissue disappears in the internode with the exception of a peripheral portion. It is rarely persistent (species of *Coriandrum*, *Eryngium*, *Ferula*, *Laserpitium*, *Sison*, and *Sium*), but this occurs both in species with

medullary vascular bundles (*Laserpitium*) as also in those without them (*Eryngium*).

4. Structure of the Root. The distribution of the resin-canals in the root of the Umbelliferae and the consequent peculiar mode of origin of the lateral roots have already been mentioned above in the general discussion of the resin-canals. It only remains now to discuss some cases of anomalous root-structure occurring in the Order. Most important of these is the structure of the napiform adventitious roots of some species of *Oenanthe*, which has repeatedly formed the subject of discussion by Behuneck, Courchet and Géneau de Lamarlière. The anomaly is most fully developed in *Oenanthe crocata*, L., where it has been investigated developmentally by Behuneck. A transverse section through a mature root of *O. crocata* shows numerous concentric vascular bundles (with central xylem), which are arranged in 2 or 3 concentric rings. If the young root of this plant is examined, normal root-structure is found; viz. around the pith there are 5–14 groups of vessels, about equidistant from one another and centripetal in their development, and between them a corresponding number of groups of soft bast occur. Soon, however, each group of vessels becomes surrounded by an envelope of many-layered cambial tissue, which on its inner side forms a few new vessels and prosenchymatous cells, subsequently lignified, and on its outer side produces a considerable amount of parenchymatous tissue; in this way the so-called concentric vascular bundles arise. When the first ring of concentric vascular bundles is complete, a second ring consisting of groups of vessels is developed internally; these are entirely separate from the bundles, and from them a second ring of concentric strands originates; still further to the interior new groups of vessels arise, and from these concentric bundles are again formed. As a consequence of this successive mode of development the bundles of the outermost ring are most strongly differentiated. According to Courchet, *Oenanthe globulosa* (Fig. 97) has a structure similar to that of *O. crocata*. Other species, such as *O. fistulosa*, L., *O. silaifolia*, Bieb., and also, according to Courchet, *O. pimpinelloides*, likewise exhibit concentric strands, but only produce one ring, consisting of a few bundles; their development is analogous to that occurring in *O. crocata*. Similar structural features to those found in the species of *Oenanthe* named have also been observed by Géneau de Lamarlière in numerous other members of the Order (*Anthriscus sylvestris*, *Angelica sylvestris*, *Apium graveolens*, *Carum verticillatum*, *Chaerophyllum bulbosum*, *Cicuta virosa*, *Daucus Carota*, *Sium latifolium*). Another anomaly occasionally, but not always, appears in older roots of *Myrrhis odorata*, according to Trécul. Its charac-

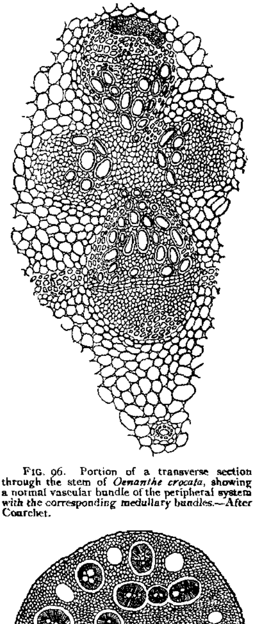

Fig. 96. Portion of a transverse section through the stem of *Oenanthe crocata*, showing a normal vascular bundle of the peripheral system with the corresponding medullary bundles.—After Courchet.

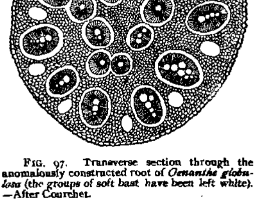

Fig. 97. Transverse section through the anomalously constructed root of *Oenanthe globulosa* (the groups of soft bast have been left white). —After Courchet.

teristic feature consists in the appearance of accessory meristematic rings in the secondary xylem of the root and the development of inversely orientated rings of bundles or of bast from these secondary meristems (for details on this point see Trécul and the abstract in De Bary, p. 624).

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ARALIACEAE.

1. Review of the Anatomical Features. Schizogenous secretory canals, which occur in the pith and throughout the cortex of the axis, but are confined to the veins in the leaf, are common to all the members of the Order. It is noteworthy that the resin-canals of the root are generally situated opposite the groups of both primary xylem and primary bast of the fibro-vascular system, and as a consequence an exceptional displacement of the young lateral roots takes place. A stomatal type characteristic of all the members of the Order is not present. The wood contains (*a*) vessels with perforations, which are simple and elliptical or scalariform with few bars, and (*b*) simple-pitted wood-prosenchyma, which is occasionally septate; the vessels, where

they are in contact with parenchyma, possess large simple pits with transitions to bordered pits. The development of cork takes place superficially in the few cases investigated. Oxalate of lime is excreted especially in the form of clustered crystals, rarely of solitary crystals. Gelatinization of the epidermis of the leaf has not been observed. As special secretory elements, in addition to the canals mentioned above, only schizogenous secretory cavities are found; the latter characterize the genus *Gilibertia*, and commonly give rise to transparent dots in the leaf. The hairy covering (Fig. 98) varies, and includes the following types: shaggy hairs, consisting of several rows of cells, and in some cases having a glandular function (*Acanthopanax, Aralia, Eleutherococcus, Fatsia, Panax, Pentapanax, Schefflera*); uniseriate glandular hairs, which are rare (*Fatsia*); tufted hairs (*Brassaia, Heptapleurum, Trevesia*); stellate hairs with unicellular rays (*Astrotricha, Fatsia, Hedera, Oreopanax*); stellate hairs with uniseriate rays (*Brassaiopsis, Heptapleurum*); peltate hairs (*Hedera*); finally two-armed hairs with a uniseriate stalk (*Didymopanax* and *Sciadophyllum*). A number of anatomical features in the leaf-structure are important in specific diagnosis, viz.: formation of papillae on the lower epidermis of the leaf; development of hypoderm on the upper side of the leaf; structural features of the cuticle, such as cuticular ridges; occurrence of arm-palisade parenchyma, &c. The occurrence of medullary vascular bundles is characteristic of certain species of *Aralia* and *Arthrophyllum*: these bundles are mostly arranged in a ring; they have collateral structure and are inversely orientated with regard to the position of their wood and bast.

2. STRUCTURE OF THE LEAF. Regarding the leaf-structure of the Araliaceae no observations have so far been published. The following account is based on unpublished investigations by Dr. O. Bachmann [1], which were undertaken at an earlier date in the botanical laboratory of the university of Munich, and on an examination of his preparations.

The leaves of the Araliaceae, as far as they have been investigated, show bifacial structure throughout. The palisade-tissue usually consists of long cells, rarely of short cells; the spongy tissue is loose. Arm-palisade parenchyma differentiated in a well-marked manner is present in species of *Acanthopanax*, *Gilibertia*, and *Cussonia*. The **stomata** are always found on the lower side of the leaf only. There is no type of stoma common to all the members of the Order, although special subsidiary cells sometimes accompany the guard-cells; but this feature on the whole is only of specific value. In *Acanthopanax innovans*,

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[1] The following species were examined: *Aralia armata*, Seem., *A. canescens*, Sieb. et Zucc., *A. californica*, Nutt., *A. chinensis*, L., *A. cissifolia*, Griff., *A. dasyphylla*, Miq., *A. edulis*, Sieb. et Zucc., *A. foliolosa*, Seem., *A. hypoleuca*, Presl., *A. laetevirens*, Gay, *A. nudicaulis*, L., *A. Pseudoginseng*, Benth., *A. racemosa*, L., *A. spinosa*, L., *A. Thomsoni*, Seem.; *Pentapanax Leschenaultii*, Seem., *P. racemosum*, Seem., *P. subcordatum*, Seem.; *Acanthopanax aculeatum*, Seem., *A. divaricatum*, Sieb. et Zucc., *A. innovans*, Franch. et Sav., *A. pentaphyllum*, March., *A. sessiliflorum*, Seem., *A. spinosum*, Miq.; *Astrotricha floccosa*, DC., *A. ledifolia*, DC.; *Fatsia horrida* (Sm.), Benth. et Hook., *F. japonica*, Decne. et Planch., *F. papyrifera*, Benth. et Hook.; *Panax arboreum*, Forst., *P. elegans*, F. v. Müll., *P. quinquefolium*, L., *P. repens*, Maxim., *P. sambucifolium*, Sieb., *P. trifolium*, L.; *Didymopanax longepetiolatum*, March., *D. macrocarpum*, Seem., *D. Morototoni*, Decne. et Planch., *D. Spruceanum*, Seem., *D. valdiviense*, Baill., *D. vinosum*, March.; *Schefflera digitata*, Forst.; *Sciadophyllum Brownii*, Spreng., *S. japurense*, Mart. et Zucc.; *Eleutherococcus senticosus*, Maxim.; *Pseudopanax crassifolium*, Koch; *Heptapleurum abyssinicum*, Benth. et Hook., *H. aromaticum*, Benth. et Hook., *H. corona-sylvae*, Benth. et Hook., *H. elatum*, Clarke, *var. Griffithii*, Clarke, *H. glaucum*, Clarke, *H. heterophyllum*, Seem., *H. Khasianum*, Clarke, *H. racemosum*, Bedd., *H. rostratum*, Bedd., *H. stellatum*, Gaertn., *H. venulosum*, Seem.; *Gilibertia cuneata*, March., *G. laurifolia*, March., *G. resinosa*, March.; *Trevesia palmata*, Vis.; *Cussonia spicata*, Thunb., *C. thyrsiflora*, Thunb.; *Heteropanax fragrans*, Seem.; *Brassaiopsis Griffithii*, Clarke, *B. ricinifolia*, Seem.; *Arthrophyllum javanicum*, Bl.; *Dendropanax arboreum*, Decne. et Planch., *D. japonicum*, Seem., *D. pendulum*, Decne. et Planch., *D. samydaefolium*, March.; *Brassaia capitata*, Clarke; *Hedera colchica*, Koch, *H. Helix*, L.; *Oreopanax capitatum*, Decne. et Planch., *O. xalapense*, Decne. et Planch.; *Macropanax oreophilum*, Miq., *M. undulatum*, Seem.

for example, subsidiary cells are present, and are placed parallel to the pore as in the Rubiaceae, but this is not the case in *Acanthopanax aculeatum* and other species. In *Didymopanax macrocarpum*, *D. Morototoni*, *D. vinosum*, and in part also in *D. longepetiolatum* subsidiary cells parallel to the pore are likewise present, but not in *D. Spruceanum*. In the same way it is only in certain species of *Brassaiopsis* and *Gilibertia* that the guard-cells are wedged in between three subsidiary cells. The **epidermis** of the leaf affords many characters for specific diagnosis. The thickness of the outer and lateral walls of the epidermal cells often varies greatly, as also does the outline of the lateral walls. The differentiation of the cuticle is also of value for specific diagnosis. It may be mentioned here in illustration of this point that in the epidermis on the lower side of the leaf of *Sciadophyllum Brownii* the cuticle has torose thickenings, that the guard-cells of *Heptapleurum stellatum* and *H. venulosum* exhibit cuticular ridges, and that *H. glaucum* shows serrated cuticular crests of considerable size, on the lower side of the leaf; to this feature the glaucous appearance of the lower leaf-surface in the latter species is due. In *Panax arboreum* thin vertical walls are found in the epidermis of the upper side of the leaf. Other features, characteristic of certain species, are the occurrence of **hypoderm** beneath the upper epidermis and the formation of papillae on the lower epidermis. Hypoderm varying in its degree of differentiation is found in the following species: *Pentapanax Leschenaultii* (locally), *P. racemosum*; *Panax arboreum* (locally), *P. elegans*; *Didymopanax macrocarpum* (two-layered, undulated and sclerenchymatous), *D. Morototoni*, *D. Spruceanum*, *D. vinosum*; *Sciadophyllum Brownii*, *S. japurense*; *Pseudopanax crassifolium* (two-layered, collenchymatous); *Heptapleurum abyssinicum*, *H. corona-sylvae* (one-layered and composed of enormous cells), *H. heterophyllum*, *H. Khasianum*, *H. racemosum*, *H. rostratum*, *H. stellatum*, *H. venulosum*; *Cussonia spicata*, *C. thyrsiflora*; *Arthrophyllum japonicum*; *Dendropanax pendulum*, *D. samydaefolium*; *Oreopanax capitatum*. With regard to the formation of papillae on the lower side of the leaf, those of *Aralia cissifolia* are short; in *Aralia canescens*, *A. chinensis*, *A. hypoleuca* and *A. spinosa*, on the other hand, the papillae are long, provided with a small crown at their apex, striated superficially and united to one another by cuticular ridges, which stand out at right angles to the surface of the leaf. Gelatinization of the epidermis of the leaf has not been observed in any member of the Order. The vascular bundles in the **veins** of the leaf are sometimes accompanied by sclerenchyma, which occasionally forms a ring round the vascular system; in many cases, however, the sclerenchyma is wanting. From a systematic point of view it is only of specific value.

Oxalate of lime in the leaf is chiefly differentiated in the form of clustered crystals, which occur both free in the mesophyll and also in the ground-tissue and bast of the veins, rarely (*Heptapleurum corona-sylvae* and *H. elatum*) in the epidermis. The excretion of oxalate of lime in the form of solitary crystals is not common, and in the cases known (species of *Heptapleurum* and *Brassaiopsis*) is confined to the neighbourhood of the veins [1].

As **secretory organs** schizogenous secretory canals and secretory cavities are found in the leaf. The secretory canals are present in all the members of the Order. In the leaf they are confined to the veins, and never run freely in the mesophyll; as a rule they also follow the finer branches of the veins. According to Trécul, *Panax Lessonii* and *P. crassifolium* constitute a noteworthy exception to this, for in these plants the resin-canals are only present in the median vein of the leaf. In the veins the secretory canals are found

[1] At this point we may refer to the occurrence of crystalloids, which Zimmermann met with in the chloroplasts of the epidermis in the petiole of *Aralia Sieboldii* and *Hedera Helix*.

both in the bast of the vascular bundles and in the ground-tissue. The width of the resin-canals can without doubt be employed in specific diagnosis. In certain species of the genus *Aralia*, for example, the resin-canals situated in the ground-tissue of the veins have very wide but in others very narrow lumina. Secretory cavities are characteristic of the genus *Gilibertia*; they mostly give rise to distinct transparent dots. Their origin, like that of the resin-canals, is schizogenous, and consequently they are lined with a one-

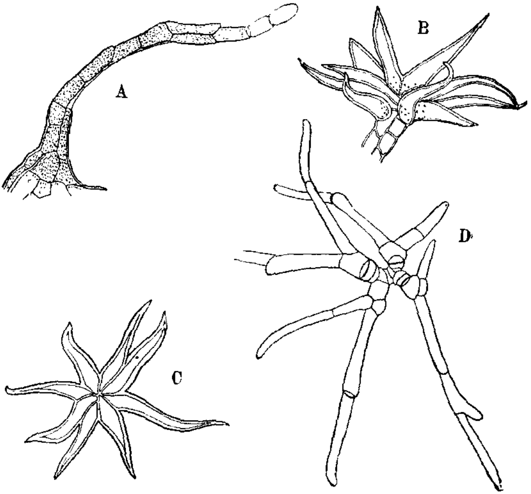

FIG. 98. Hairs of some Araliaceae: A, Shaggy hair of *Aralia californica*, Nutt. B, C, *Hedera Helix*, L. (B) Tufted hair and (C) small scale-like trichome. D, Star-like trichome of *Trevesia palmata*, Vis.—Original.

layered epithelium. Harms has recently demonstrated these secretory cavities in a large number (eleven) of American species of *Gilibertia*, as well as in *Gilibertia japonica* (Seem.), Harms, but not in *G. Protea* (Benth.), Harms (endemic in Hong-Kong). The latter plant, therefore, requires re-examination in relation to its inclusion in the genus *Gilibertia*.

The **hairy covering** (Fig. 98) varies. In most cases the leaves are glabrous; but in that case a hairy covering is occasionally to be found in the floral region. The trichomes to be first described are the shaggy hairs (in species of *Aralia, Acanthopanax, Pentapanax, Panax, Eleutherococcus*, and in *Fatsia horrida*). They consist, at least in their lower portion, of several rows of cells; they vary in length, and may be either pointed or blunt. In some species of *Aralia* (*Aralia californica*, Fig. 98, *A*, *A. edulis*, and perhaps also in *A. racemosa*) these shaggy hairs seem to have a glandular function, as is indicated by the thin walls of the uppermost cells. Other forms of glandular hairs occurring in the Order are: very short shaggy hairs (*Schefflera*

digitata) and very short, uniseriate, finger-shaped glandular hairs (*Fatsia japonica*). The genera *Didymopanax* and *Sciadophyllum* possess two-armed trichomes with a uniseriate stalk, composed of short cells, and a terminal cell with equal arms, which is either thickened uniformly on all sides (*Didymopanax macrocarpum*) or only on the side of the wall adjoining the leaf-surface (*D. longepetiolatum*). Tufted **hairs** composed of unicellular, thin-walled trichomes have been met with in the floral region of species of *Heptapleurum* and *Brassaia capitata*; tufted or stellate hairs with a uniseriate or multiseriate stalk and unicellular rays occur in *Astrotricha, Fatsia papyrifera, Hedera Helix* (Fig. 98, *B*), and *Oreopanax xalapense*; peltate hairs are found in the genus *Hedera*. In *Hedera Helix* (Fig. 98, *C*) the shield of these hairs is composed of thick-walled ray-cells, which almost meet at the centre of the disc; in *Hedera colchica* it is formed of thin-walled ray-cells, which abut on one another along a median line and form conical elevations at the centre of the shield. A special type of stellate hair with thin walls and uniseriate rays (Fig. 98, *D*) is found in the floral region of *Heptapleurum elatum* and *Brassaiopsis Griffithii*, and on the leaf of *Trevesia*. Ordinary unicellular hairs have not been observed in this Order; on the other hand, uniseriate trichomes, which have thin walls and are occasionally slightly branched, are found in *Cussonia thyrsiflora*.

The **petiole** has been examined by Petit and Plitt in species of *Aralia, Fatsia, Hedera, Heptapleurum, Meryta* and *Panax*. The vascular bundles of the petiole are mostly isolated or their bast-portions only are united; the number of the vascular bundles varies. *Aralia spinosa, Heptapleurum* (*Paratropia*) *venulosum*, Seem. and *Meryta* (*Botryodendron*) *macrophylla*, Seem. possess two rings of bundles in the characteristic region ('caractéristique'); the vascular bundles of the outer ring are normally orientated with regard to the position of wood and bast, and are alternately of large or small size, those of the inner ring being inversely orientated and placed opposite to the smaller bundles of the outer ring. *Fatsia horrida* also has two rings of vascular bundles in the petiole, but in both the bundles are normally orientated. A woody species of *Hedera*, of which Petit does not give the specific name, may also be mentioned, because its petiole exhibits, in the characteristic region, an arc of isolated vascular bundles and an upper ring of wood and bast.

The occurrence of cork-warts on the petiole of *Aralia papyrifera* and *A. Sieboldii* may be noted (Borzi).

3. Structure of the Axis. Most investigations dealing with the structure of the axis in the Araliaceae have had in view the demonstration and arrangement of the **secretory canals**; these canals are present in all the members of the Order, and are filled with oily and resinous, gummy, or occasionally milky contents. For the purposes of this book it must suffice to mention that the development of the canals takes place schizogenously, and that they are met with in all parts of the cortex [1] (both in the bast and primary cortex), and often also in the pith [2]. In connexion with this point reference may be made to the position of the secretory canals in the roots; according to Van Tieghem they are formed in the pericambium opposite the middle of the xylem-groups of the fibro-vascular system, but in addition to these supravasal canals a secretory canal may also arise in the pericambium opposite each phloem-

[1] According to Trécul the resin-canals of the bast and outer cortex in *Paratropia macrophylla* exhibit an undulated course in the radial direction combined with anastomoses.

[2] Medullary resin-canals are found according to Trécul: in *Aralia edulis* and *A. racemosa* scattered in the pith, in *A. chinensis* in the periphery and in small numbers in the interior of the pith, in *A. spinosa, Cussonia thyrsiflora, Hedera Helix, Panax Lessonii* and *Paratropia macrophylla* solely in the periphery of the pith. *Fatsia horrida*, Benth. et Hook. and *Aralia pentaphylla*, Thunb., on the other hand, have no medullary resin-canals.

group. The exceptional displacement of the young lateral roots is a consequence of this arrangement; they arise in each interspace between a supravasal canal and the neighbouring secretory canal, opposite the phloem, i.e. they are produced in double the usual number. (Regarding the secretory canals of the veins of the leaf, see above; regarding those of the petiole, see Trécul and K. Müller.)

Another anatomical feature of the axis has repeatedly formed the subject of investigation (by Trécul, Cedervall, and J. E. Weiss), viz. the occurrence of **medullary vascular bundles**. These have been observed in the following species: by Trécul, in *Aralia edulis* and *A. racemosa*; by Sanio, in *Aralia racemosa* and *A. japonica*; by Cedervall, in *Aralia edulis, A. hispida, A.* '*indica,*' *A.* '*kaschemirica,*' *A. nudicaulis*; by Van Tieghem, in *Arthrophyllum*[1] *diversifolium* and *A. ellipticum*. The absence of medullary bundles has been demonstrated in: *Aralia crassifolia, A. dasyphylla, A. palmata, A. papyrifera, A. pentaphylla, A. Sieboldii, A. spinosa,* and *A. umbraculifera; Cussonia thyrsiflora; Dimorphanthus mandshuricus; Fatsia horrida; Hedera Helix; Macropanax oreophilum; Panax dendroides, P. fragrans, P. fruticosum* and *P. Lessonii; Paratropia macrophylla* and *P. venulosa; Sciadophyllum Brownii* (see Trécul, Sanio, Cedervall, Solereder, loc. cit.). The medullary bundles are generally arranged in a ring; they have collateral structure and are inversely orientated, i.e. the bast is directed towards the centre of the pith, and the xylem lies on the outside. In addition to these vascular bundles, which form a ring, irregularly orientated bundles are occasionally found in the inner portion of the pith (*Aralia edulis, A.* '*indica*' and *A. racemosa*). According to Cedervall, these latter bundles exhibit concentric differentiation in *A. racemosa* and *A.* '*indica,*' the phloem being situated in the centre. In the case of the medullary vascular bundles of *Aralia edulis* and *A. racemosa*, J. E. Weiss has shown that they first run as normal bundles in the peripheral ring and only enter the pith subsequently, at the same time undergoing a rotation through 180°.

The structure of the **cortex** has only been examined in *Panax* sp., *Aralia japonica*, Thunb., *Hedera Helix*, L., and *Aralia pentaphylla*, Thunb. by Möller. The following are characteristic features of the cortex of these plants, in addition to the occurrence of the secretory canals, which have already been discussed: the cork-cells are sclerosed on one side only in certain layers of the periderm; stone-cells are wanting in *all* parts of the cortex; of rare occurrence (at least in branches of the thickness of a finger) are: (1) short bast-fibres differentiated after the manner of rod-cells, (2) chambered crystal-fibres with clustered crystals, and (3) broad medullary rays. The development of the periderm takes place in the outermost cell-layer of the cortex.

Regarding the structure of the **wood** the following facts may be mentioned, based on an investigation of *Fatsia horrida*, Benth. et Hook., *Hedera Helix*, L. and *Aralia pentaphylla*, Thunb., and more recently of *Gilibertia cuneata*, March. The transverse section of the wood usually shows broad medullary rays, which may be as much as five cells in breadth, and become still broader in the later growth of the wood in *Hedera Helix*, and vessels which vary in their arrangement and in the width of their lumina (the latter in *Hedera Helix* with a diameter of ·035 mm.). The perforations of the vessels are mostly simple and elliptical; their elongated elliptical shape in *Hedera* and *Aralia*, however, as well as the occurrence of a few bars in *Gilibertia* and *Fatsia*,

[1] The occurrence of medullary bundles in *Arthrophyllum*, together with the presence of secretory canals in this genus, is regarded by Van Tieghem and Sertorius as evidence for the inclusion in the Araliaceae of *Arthrophyllum*, which is placed in the Cornaceae by some authors (Seemann for example). Three other genera (*Mastixia, Curtisia, Helwingia*), which are referred to the Araliaceae by some, but must be included in the Cornaceae, will be mentioned in the description of the last-named order.

indicate a transition to scalariform perforation; the division-walls of the segments of the vessels are more or less strongly inclined. Those walls of the vessels which abut on parenchyma of the medullary rays as a rule bear large, simple, elliptical pits, and, accompanying the latter, transitions to bordered pits. The wood-prosenchyma has simple pits. In *Hedera Helix* and *Aralia pentaphylla* delicate division-walls occasionally appear in the wood-prosenchyma, and hand in hand with this goes the occurrence of starch.

The structure of the **pith** has only been examined in detail in *Aralia spinosa* by Mentovich. In this plant the pith is empty ('moelle inerte' of Gris), but contains crystal-cells.

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CORNACEAE.

1. Review of the Anatomical Features. The leaves of the Cornaceae are distinguished by the lack of characteristic subsidiary cells accompanying the guard-cells, whilst the axis is characterized by the scalariform perforations of the vessels, which often have numerous bars; the genera *Alangium, Marlea* pro parte and *Toricellia* alone exhibit simple perforations in the secondary wood, but scalariform septa are also to be found in these plants in the neighbourhood of the primary vessels.

The wood generally consists of (*a*) isolated vessels with small lumina, of quadrangular shape in transverse section; (*b*) wood-prosenchyma, which bears bordered pits only in *Cornus, Garrya, Camptotheca, Curtisia, Davidia,* and *Mastixia,* simple pits only (being at the same time occasionally septate) in *Alangium, Marlea, Toricellia* and *Helwingia,* both simple and bordered pits in *Aucuba, Corokia, Griselinia,* and *Nyssa*; (*c*) a small amount of wood-parenchyma; and (*d*) medullary rays 2-5 cells thick. At the outer limit of the bast isolated groups of bast-fibres, only wanting in a few cases, are generally present, or in their place a composite and continuous ring of sclerenchyma is developed (the latter in the genera *Curtisia, Griselinia, Nyssa,* and *Davidia*). Groups of secondary bast-fibres are only found in *Mastixia.* The development of cork is superficial. Oxalate of lime is usually excreted in the form of clustered crystals, but also in that of solitary crystals, and occurs as crystal-sand in the genera *Aucuba, Garrya,* and *Toricellia.* Of secretory organs, cells filled with a secretion are found in the veins of the leaf of *Nyssa,*

while medullary secretory canals occur in *Mastixia*. The hairy covering (Fig. 99) generally consists of simple unicellular hairs of varying length, unicellular hairs bent in the form of a hook (*Marlea*), unicellular (*Cornus*, *Mastixia*) or two-celled (*Corokia*) two-armed hairs, and glandular hairs of varied structure (only in *Alangium*, *Marlea*, *Nyssa*, *Camptotheca* and *Toricellia*). The simple hairs are sometimes provided with verrucose thickenings; the walls of the two-armed hairs in some cases bear similar thickenings, and are encrusted with carbonate of lime.

Finally, a number of special anatomical features are of importance in specific diagnosis, e.g.: formation of papillae on the epidermis of both sides of the leaf; occurrence of hypoderm on the upper side; gelatinization of the epidermis of the leaf; spicular cells in the mesophyll (Fig. 99, *A*); clustered crystals in the epidermis of the leaf; special crystal-idioblasts in the leaf-tissue; spiral thickening of the walls of the vessels; bast-fibres with yellow or white walls, &c.

2. STRUCTURE OF THE LEAF [1]. The leaves as a rule have bifacial structure. The palisade-tissue usually consists of a single layer of cells; the spongy tissue is generally loose. With regard to the **epidermis** of the upper side of the leaf the following facts may be pointed out. The cells are never of any considerable size, and they vary in the thickness and markings of their outer walls (striated, rarely granular thickenings) and in the form of the lateral margins. In *Helwingia* those walls which are perpendicular to the leaf-surface project into the cell-cavities in the form of humps at many points along the circumference of the cells. Formation of papillae has been observed in: *Garrya elliptica*, Dougl., *G. flavescens*, Wats., *G. laurifolia*, Benth., *G. Lindheimeri*, Torr., *G. ovata*, Benth. and *G. Wrightii*, Torr., *Marlea begoniaefolia*, Roxb., *M. macrophylla*, Sieb. et Zucc. and *M. platanifolia*, Sieb. et Zucc. and *Cornus canadensis*, L.: the papillae of *Garrya Wrightii* are solid, differing in this respect from those of the other species; they therefore appear as peg-like thickenings of the outer wall. **Hypoderm** is developed on the upper side of the leaf in *Garrya buxifolia*, A. Gray, *G. elliptica*, Dougl. and *G. flavescens*, Wats., *Griselinia jodinifolia*, Taub., *G. littoralis*, Raoul and *G. lucida*, Forst and *Marlea nobilis*, Clarke; in the species of *Garrya* and *Griselinia* the cells of the hypoderm exceed those of the epidermis in size. A tendency towards the formation of a hypoderm is found in *Marlea ebenacea*, Clarke, where the epidermal cells, which are elongated almost like a palisade, exhibit transverse walls, more or less parallel to the leaf-surface. Gelatinization of the upper epidermis of the leaf has been met with in *Cornus excelsa*, H. B. K., *C. ignorata*, Koch, *C. mas*, L. (Walliczek) and *C. stricta*, Lam., *Nyssa capitata*, Walt., *N. caroliniana*, Poir., *N. multiflora*, Wang., *N. uniflora*, Wang. and *N. villosa*, Michx. and *Camptotheca acuminata*, Decne. The epidermal cells on the lower side of the leaf show similar variations to those of the upper side in relation to the marking on the outer walls, the lateral margins and the formation of papillae. Sertorius states that a slight formation of papillae occurs in species of *Garrya*, *Aucuba*, *Nyssa*, *Toricellia*, and *Cornus*, whilst *Garrya Wrightii*, Torr. possesses the same type of solid papillae as occurs on the upper side, and many species of *Cornus* [2] have long papillae, which exhibit a prominent longitudinal striation, terminate in a jagged crown, and are united to one another by vertical cuticular ridges. The **stomata** are not accompanied by special subsidiary cells, and are in almost all cases confined to the lower side of the

[1] The following description of the structure of the leaf and axis is mainly based on the work of Sertorius, who examined about 70 species of the 14 genera, which are repeatedly named below.

[2] These are:—*C. alba*, L., *C. brachypoda*, C. A. Mey., *C. californica*, C. A. Mey., *C. capitata*, Wall., *C. circinnata*, L'Hérit., *C. disciflora*, DC., *C. ignorata*, Koch, *C. macrophylla*, Wall., *C. oblonga*, Wall., *C. paniculata*, L'Hérit., *C. pubescens*, Nutt., *C. sibirica*, Loddy.

leaf; in *Marlea begoniaefolia* alone they are also present on the upper side in the neighbourhood of the veins.

In the structure of the larger **veins** the following facts may be noted. No sclerenchyma is differentiated in them in the genera *Aucuba*, *Camptotheca*, *Davidia*, *Toricellia*, *Helwingia*, *Cornus* (with the exception of *C. disciflora*, DC., *C. florida*, L., *C. stricta*, Lam. and *C. tolucensis*, H. B. K.), further in *Griselinia racemosa*, Taub. and *G. scandens*, Taub., *Nyssa grandidentata*, Michx., *N. multiflora*, Wang. and *Corokia Cotoneaster*, Raoul. Sclerenchymatous fibres with thick walls and narrow lumina accompany the vascular bundles of the larger veins in the genus *Alangium*, in *Marlea ebenacea*, Clarke, and *M. nobilis*, Clarke, in *Corokia buddleioides*, A. Cunn., and in the genus *Garrya*. In *Mastixia* a sclerenchymatous ring surrounds the vascular system. In the remaining genera (or species, as the case may be), groups of sclerenchymatous fibres with relatively wide lumina are generally present accompanying the vascular system. The vascular bundles of the smaller veins are as a rule embedded. Vertically transcurrent veins, i.e. lateral veins of a higher order, the vascular system of which is connected with the upper and lower epidermis by usually thin-walled tissue, are found in various genera, and especially in all investigated species of the genus *Nyssa*.

A special anatomical feature of the leaf-structure is the occurrence of sclerenchymatous cells in the **mesophyll** (species of *Garrya*, *Griselinia*, and *Nyssa*). In *Griselinia lucida*, Forst. rounded cells with a wide lumen and a sclerosed and pitted wall are found in the spongy tissue. Sclerenchymatous cells, which run freely in the mesophyll and are sometimes branched, occur in various forms in some species of *Garrya* (*G. buxifolia*, Gray, *G. elliptica*, Dougl., *G. Fadyenii*, Hook., *G. flavescens*, Wats. var., *G. laurifolia*, Benth.), whilst these elements are replaced by slightly thickened sclerenchyma-cells in *G. ovata*, Benth. and *G. Lindheimeri*, Torr., and are wanting in *G. Wrightii*, Torr. Finally, the spicular fibres of *Nyssa caroliniana*, Poir. (Fig. 99, *A*), *N. multiflora*, Wang. and *N. villosa*, Michx. (in *N. caroliniana* giving rise to transparent dots in the leaf) traverse the entire leaf perpendicularly to the surface, are scarcely branched, and occasionally penetrate between the epidermal cells, sometimes even extending beyond them and producing elevations in the cuticle.

Oxalate of lime is excreted in the form of clustered crystals, solitary crystals, or crystal-sand. The clustered crystals are by far the most abundant. Those in the mesophyll are occasionally of considerable size, as in *Alangium* and *Marlea* (*M. begoniaefolia*, Roxb. and *M. platanifolia*, S. et Z.), being specially large in *M. begoniaefolia*, where they extend from the epidermis on one side to that on the other surface, and give rise to transparent dots in the leaf. In many species of *Cornus* groups of 3–5 clustered crystals are situated beneath the palisade-tissue, a feature which is readily observed on examination of bleached portions of the leaves of the species in question. In the lower epidermis of the leaf small clustered crystals have only been observed in *Alangium hexapetalum*, Lam., *Marlea nobilis*, Clarke, and *Griselinia lucida*, Forst. The occurrence of solitary crystals in the leaf-parenchyma (with the exception of that in the neighbourhood of the veins) is comparatively rare (*Curtisia*, *Camptotheca*, *Davidia*, *Marlea ebenacea*, Clarke); in *Curtisia* and *Camptotheca* the solitary crystals attain especially large dimensions. Accompanying the vascular bundles of the veins we find clustered crystals, alone or together with solitary crystals, but never the latter only. A third and specially noteworthy mode of excretion of oxalate of lime is that of crystal-sand, which is characteristic of the genera *Aucuba*, *Garrya* and *Toricellia*, and is found in the leaf especially in the neighbourhood of the vascular bundles of the veins. Lastly, we may mention the fact that in the genera *Toricellia*, *Hel*-

wingia, *Corokia* and in certain species of *Cornus*, *Marlea* and *Nyssa*, excretion of oxalate of lime does not take place at all in the leaf.

Among the **secretory elements** one meets with secretory canals in the medullary portion of the larger veins of *Mastixia*; these canals will be discussed more fully in describing the structure of the axis. In species of *Nyssa* secretory cells, not differentiated as idioblasts, are occasionally found in that part of the tissue of the vertically transcurrent veins, which abuts on the vascular bundles. In some species organized fat-bodies, some of which are doubly refractive, occur in the dried leaf (species of *Alangium*, *Cornus*, *Corokia*, and *Garrya*).

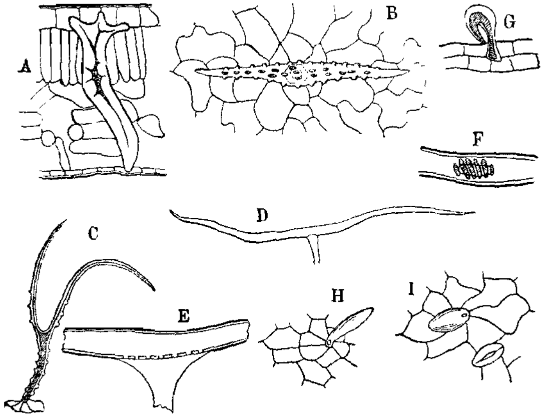

FIG. 99. A, Portion of a transverse section of the leaf of *Nyssa Caroliniana*, Poir. B, C, Two-armed trichomes of *Cornus Nuttallii*, Audub.: B, trichome with equal arms from the upper side of the leaf, C, a similar hair but Y-shaped from the lower side of the leaf. D–F, Two-celled, two-armed trichomes of *Corokia*: D, *Corokia Cotoneaster*, Raoul; E, F, *C. buddleioides*, A. Cunn.: E, central portion of the trichome, F, wall between the stalk and the two-armed terminal cell, in surface-view. G, Hook-shaped hairs of *Marlea nobilis*, Clarke. H, I, External glands: H, *Nyssa Caroliniana*, Poir., I, *Camptotheca acuminata*, Decne.—Original.

The following three forms of **trichomes** (Fig. 99) occur on the leaf: simple, unicellular hairs, two-armed hairs (only in *Cornus*, *Corokia* and *Mastixia*) and glandular hairs (only in *Alangium*, *Marlea*, *Nyssa*, *Camptotheca* and *Toricellia*). Without going into details, which can be obtained from Sertorius's work, it may first be pointed out that the simple hairs vary in the thickness of their walls and in their length. For example, short trichomes are found in *Alangium glandulosum*, Thw., whilst long ones, which are much undulated and form a dense felt on the lower side of the leaf, occur in *Curtisia* and species of *Garrya*. The walls of the simple, unicellular hairs are in many cases (*Griselinia*, *Nyssa*, *Camptotheca* and *Davidia*) provided with granular, verrucose or nodular prominences, into which the cell-lumen occasionally penetrates. A special form among the ordinary unicellular trichomes is constituted by the hairs of the species of *Marlea* (Fig. 99, *G*), which resemble an angler's hook; these hairs are in some cases sunk in small pits on the leaf-surface. Ordinary,

uniseriate hairs are almost entirely wanting in the Order; it is only in the unicellular trichomes of the floral region of *Toricellia* that the formation of a transverse wall has now and then been observed. The two-armed hairs are unicellular in *Cornus* and *Mastixia*; in *Cornus* (Fig. 99, *B–C*) the wall of these hairs is encrusted with carbonate of lime. The shape of the two-armed hairs in this genus varies (hairs with arms of equal or almost equal length; hairs with very unequal arms; others in which one arm is only differentiated as a short spur; hairs with lyrate arms; Y-shaped hairs; one-armed hairs); these characters may probably be occasionally employed for specific diagnosis. The two-armed hairs, which form the shining tomentum on the lower side of the leaf in *Corokia buddleioides*, A. Cunn. and *C. Cotoneaster*, Raoul (Fig. 99, *D–F*), certainly consist of more than a single cell, and in this respect differ from the trichomes of *Cornus* and *Mastixia*. Sertorius describes them as two-celled, one of the cells belonging to the stalk, while A. Weiss states that he has observed 4 or 5 stalk-cells in living material of the first-named species. It may be added that this author also met with an incrustation of carbonate of lime in the walls of the hairs in his material. The hairs of *Corokia* are especially distinguished (Fig. 99, *E–F*) by the occurrence of elliptical pits on that portion of the wall which is common to the stalk and the transverse cell of the hair, these pits being arranged in such a way that, taken together, they recall a scalariform perforation with few bars. With regard to the differentiation of the glandular hairs it may be mentioned that *Toricellia* possesses small curved hairs of 3–4 cells, whilst *Alangium, Marlea, Nyssa* and *Camptotheca* have unicellular external glands (Fig. 99, *H–I*, hydathodes ?), which vary in shape.

The structure of the **petiole** has been examined by Petit and Plitt in species of *Alangium, Aucuba, Cornus, Griselinia,* and *Helwingia*. In all cases three isolated vascular bundles enter the petiole. In the characteristic region (caractéristique) the fibrovascular system either forms a simple arc, or the arc is closed above by a band of wood and bast; occasionally two small vascular bundles are also present on the upper side.

3. Structure of the Axis. According to Sertorius, the cork always arises subepidermally, and is generally composed of cells with thin walls and wide lumina; according to Möller and J. E. Weiss, the epidermis sometimes becomes the phellogen (*Aucuba* and species of *Cornus*). The primary **cortex** in almost all cases (exception: *Mastixia*) is collenchymatous, either throughout or at least in its outer portion; typical collenchyma, however, only occurs in *Toricellia*. The following special features are found in the primary cortical parenchyma: cortical vascular bundles in *Mastixia*, i.e. leaf-trace strands, only entering the vascular ring lower down in the stem; stone-cells (*Mastixia, Marlea ebenacea*, Clarke, and *M. nobilis*, Clarke, *Cornus capitata*, Wall., *Nyssa uniflora*, Wang.); and, in herbarium-material of species of *Aucuba, Cornus* and *Garrya*, tangential rents in the collenchyma due to the gelatinization of the middle lamellae between the cells concerned. In the pericycle we either find (in the majority of the species) isolated bundles of primary bast-fibres, which are occasionally strengthened by the addition of stone-cells (species of *Marlea, Cornus, Mastixia, Garrya*), or a composite and continuous sclerenchymatous ring (*Curtisia, Griselinia, Nyssa* and *Davidia*), or finally no sclerenchyma at all (*Marlea begoniaefolia*, Roxb., *Helwingia, Aucuba japonica*, Thunb.). The groups of bast-fibres in the pericycle are distinguished either by the yellow (*Alangium, Corokia, Mastixia, Garrya* pro parte, *Griselinia, Nyssa, Toricellia*) or white (*Marlea, Curtisia, Cornus, Aucuba Garrya* pro parte, *Camptotheca, Davidia*) coloration of their wall; in branches belonging to the floral region these groups are usually of small size, being relatively large in *Toricellia* only; in *Mastixia* they are elongated in th

radial direction to a striking extent. In the secondary bast of branches from herbarium-material bast-fibres have only been observed in *Mastixia*, where they either occur singly or form small groups; in the bark of the trunk of *Aucuba* and *Cornus* secondary hard bast is also wanting (Möller). On the other hand parenchymatous sclerenchyma, generally with rod-like elements, has been observed in the bast in species of *Corokia, Marlea, Cornus* and *Nyssa*.

Regarding the structure of the **wood** the following facts may be pointed out. The vessels usually occur isolated in the transverse section of the branch, and are generally more nearly quadrangular than rounded in section. As a rule they have narrow lumina, which are sometimes remarkably small (diam. = ·013 mm. in *Corokia*); only in *Alangium, Marlea* and *Toricellia* does their diameter attain a more considerable size (up to ·065 mm.). The perforations of the vessels are exclusively scalariform in most of the genera (*Curtisia, Corokia, Cornus, Aucuba, Mastixia, Garrya, Griselinia, Nyssa, Camptotheca, Helwingia*), and also in *Marlea ebenacea*, Clarke, and *M. nobilis*, Clarke, of the section *Pseudalangium*. In other species of *Marlea*, as well as in *Alangium* and *Toricellia*, there are only simple, mostly elliptical, perforations in the secondary wood, although the scalariform type also occurs in the primary wood or in its neighbourhood. Scalariform perforations in the vessels thus form a universal feature in the Order. The number of bars in the scalariform perforations varies, being either very considerable (over 40, or even up to 100), as in *Davidia, Aucuba* or *Nyssa*, or small (3–5), as in *Garrya*. Spiral thickening of the vessel-wall has been observed in *Cornus oblonga*, Wall., *Aucuba japonica*, Thunb., *Garrya elliptica*, Dougl., *G. Lindheimeri*, Torr. and *Toricellia tiliaefolia*, DC. Sertorius mentions bordered pits as occurring alone on the vessel-wall where it is in contact with parenchyma of the medullary rays; this is not correct for *Griselinia* (see my 'Holzstruktur'), inasmuch as simple pits also occur in that case. The walls of the wood-prosenchyma may either bear bordered pits only (*Cornus, Garrya, Camptotheca, Curtisia, Davidia, Mastixia*), or simple pits only (*Alangium, Marlea, Toricellia, Helwingia*), or both bordered and simple pits (*Aucuba, Corokia, Griselinia, Nyssa*). In *Alangium, Marlea nobilis* and *M. ebenacea, Curtisia, Corokia, Garrya, Griselinia* and *Helwingia* the wood-prosenchyma has very thick walls and very narrow lumina, while that of other species of *Marlea*, of *Cornus, Mastixia, Aucuba, Nyssa, Camptotheca, Davidia* and *Toricellia* has wide lumina and relatively thin walls. Septation by means of delicate division-walls has been observed locally in the wood-prosenchyma of most species of *Marlea*, and delicate spiral thickening in the prosenchyma of *Aucuba, Garrya* and *Cornus oblonga*, Wall., which bears bordered pits. The wood-parenchyma is only slightly developed. The medullary rays of the wood are from two to five cells thick in transverse section.

Tupelo-wood, which is the wood of the root of species of *Nyssa*, and is used in the preparation of tupelo-sounds, is distinguished by the extremely wide lumina of its elements. The vessels, as well as the wood-prosenchyma, have a diameter of ·105 mm. The wood-fibres here, as in the wood of the stem, bear bordered pits.

The **pith**, according to Sertorius (for details see loc. cit.), exhibits various types of differentiation. Its cells either have thin and slightly lignified walls or thick walls, which are sometimes sclerosed. The cells of the pith are distinguished by special pitting of their vertical walls in the species of *Nyssa*. The pits on these walls are very numerous and the thickened portions of the membrane project strongly into the lumen of the cell, so that in section the vertical walls have the appearance of a row of beads. The pith of *Aucuba* possesses another peculiarity; in the dried (but not in the living) branch it

is split up into lamellae by a considerable number of parallel rents, appearing at very short distances from one another.

Oxalate of lime is excreted in the axis in the same three forms as in the leaf (see above). Carbonate of lime has been observed in the cavities of the vessels in the heart-wood of *Cornus sanguinea* and in the pith of the wood in the trunk of *C. mas* (Molisch). The **secretory canals**[1], which characterize the genus *Mastixia* and have already been mentioned in the description of the leaf-structure, are found in the periphery, and occasionally (*M. Gardneriana*) also in the internal portions of the pith. In branches from herbarium-material they are commonly filled with crystallized camphor.

4. Table for the determination of the genera of the Cornaceae, according to their anatomical features (after Sertorius):—

I. Perforations of the vessels in the secondary wood simple:
- 1. Sack-shaped unicellular glandular hairs on the leaf; no crystal-sand: *Alangium*, *Marlea* pro parte.
- 2. Multicellular glandular hairs on the leaf; crystal-sand in axis and leaf: *Toricellia*.

II. Perforations of the vessels in the secondary wood scalariform:
- 1. Two-armed hairs on the leaf (or in the floral region):
  - (*a*) Two-armed hairs unicellular:
    - (*aa*) Secretory canals present in the pith of the axis and of the larger veins; hairs not encrusted with carbonate of lime: *Mastixia*.
    - (*bb*) Secretory canals wanting; hairs invariably provided with an incrustation of carbonate of lime: *Cornus*.
  - (*b*) Two-armed hairs bicellular (or multicellular, according to A. Weiss); encrusted with lime according to A. Weiss, but not so according to Sertorius: *Corokia*.
- 2. Two-armed hairs wanting:
  - (*a*) Unicellular glandular hairs on the leaf:
    - (*aa*) Secretory cells in the leaf; clustered crystals only: *Nyssa*.
    - (*bb*) No secretion in the leaf; solitary and clustered crystals: *Camptotheca*.
  - (*b*) No glandular hairs on the leaf:
    - (*aa*) Crystal-sand in leaf and axis:
      - (α) Lateral walls of the epidermal cells on both sides of the leaf undulated in a zigzag manner; no sclerenchyma accompanying the vascular bundles of the veins; perforations of the vessels with numerous bars: *Aucuba*.
      - (β) Epidermal cells on both sides of the leaf polygonal in surface-view or with very slightly undulated lateral walls; bundles of sclerenchymatous fibres accompanying the vascular bundles of the veins; perforations of the vessels with few bars (number of bars 3–5, rarely as many as 10): *Garrya*.
    - (*bb*) No crystal-sand in leaf or axis:
      - (α) Leaf absolutely glabrous:
        - (αα) Leaf very thin; no hairs even in the floral region; no oxalate of lime in the mesophyll: *Helwingia*.
        - (ββ) Leaf very thick, leathery; hairs in the floral region; numerous clustered crystals in the mesophyll: *Griselinia*.
      - (β) Hairs, resembling an angler's hook, on the leaf; solitary and clustered crystals: *Marlea nobilis*, Clarke, and *M. ebenacea*, Clarke.
    - (*cc*) Only solitary crystals in the mesophyll.

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[1] The occurrence of these secretory canals led Van Tieghem to the assumption that *Mastixia* belongs neither to the Cornaceae nor to the Araliaceae, to which it is referred by Baillon, but possibly to the Dipterocarpeae. According to Sertorius's statements *Mastixia* may quite well be left amongst the Cornaceae. In this connexion it also seems advisable to point out that *Curtisia* (which is included amongst the Cornaceae by Bentham and Hooker and amongst the Araliaceae by Baillon) and *Helwingia* (referred to the Cornaceae by Baillon, but to the Araliaceae by Bentham and Hooker) have no resin-canals, and on account of this and other points should be left amongst the Cornaceae.

(α) Solitary crystals, sometimes very large and abutting on the upper epidermis; veins vertically transcurrent: *Curtisia.*

(β) Solitary crystals all of fairly large size and only present in the spongy tissue; veins not vertically transcurrent: *Davidia.*

Literature: Chalon, Anat. comp. d. tig. lign. dicotyléd., i. Mém. 1867, p. 45.—Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 66, 67 and 362.—Delbrouck, Pflanzenstach., in Hanstein, Bot. Abh., Bd. ii, 1876, p. 28.—Molisch, Kohlens. Kalk, Sitz.-Ber. Wiener Akad., Bd. lxxxiv, Abt. 1, 1881, p. 7 et seq.—Möller, Rindenanat., 1882, pp. 210–13.—Bokorny, Durchs. P., Flora 1882, p. 380, separate copy, p. 34.—Blenk, Durchs. P., Flora 1884, p. 377, and separate copy, p. 89.—H. Schenck, Centrifug. Wandverdick. an Pflanzenh., Diss., Bonn, 1884, pp. 20–2.—Van Tieghem, in Ann. Sc. nat., sér. 7, t. i, 1885, pp. 27–9 and 73–5.—Solereder, Holzstr., 1885, p. 146.—Plitt, Blattstiel, Diss., Marburg, 1886, p. 50.—Petit, Pétiole, Mém. Soc. sc. phys. et nat. de Bordeaux, sér. 3, t. iii, 1887, pp. 336–9 and pl. v.—Douliot, in Ann. sc. nat., sér. 7, t. x, 1889, p. 373.—J. E. Weiss, in Denkschr. Regensb. bot. Gesellsch. 1890, separate copy, p. 60.—A. Weiss, Trich. von *Corokia*, Sitz.-Ber. Wiener Akad., Bd. xcix, Abth. 1, 1890, p. 268 and Tab.—Brandza, Rech. anat. sur les Hybrides, Compt. rend., t. cxi, 1890, p. 317 et seq., and Revue de bot., t. ii, 1890, p. 440 et seq.—Heim, *Mastixia*, in Rech. s. l. Diptérocarp., Thèse, Paris, 1892, pp. 165–74 and pl. ix.—Sertorius, Anat. d. C., Diss., München, 1893, 78 pp.; also Bull. de l'Herbier Boissier, vol. i.—Walliczek, Membranschl., Pringsheim Jahrb., Bd. xxv, 1893, pp. 229.—Reiche, in Engler, Bot. Jahrb., Bd. xxi, 1895, p. 37.—Diels, Veg.-Biol. v. Neuseeland, Engler, Bot. Jahrb., Bd. xxii, 1896, p. 239.—Kuhla, Phelloderm, Bot. Centralbl. 1897, iii, p. 226.

CAPRIFOLIACEAE.

1. Review of the Anatomical Features. This Order is exceedingly well characterized anatomically by a number of features, viz.: the lack of a special type of stoma in almost all cases (exception: *Silvianthus*[1]); the occurrence of glandular hairs (exceptions: *Alseuosmia* and *Adoxa*); the tendency towards the formation of scalariform perforations in the vessels (exception: *Carlemannia*); and the bordered pitting of the wood-prosenchyma in most members of the Order (wood-prosenchyma with simple pits only in *Carlemannia*[1], *Sambucus* and *Alseuosmia*; accompanying prosenchyma with bordered pits in *Leycesteria*). The two first-named anatomical features are suitable for distinguishing the Caprifoliaceae from the closely-related Rubiaceae. In the general structure of the axis the following facts remain to be mentioned: the medullary rays are mostly narrow; isolated bundles of primary hard bast-fibres are almost always present at the outer limit of the bast, or are replaced by a ring of bast-fibres; secondary hard bast occurs in almost all the members of the Order in which Möller examined the details of the cortical structure (with the exception of *Viburnum*); and stone-cells (except in *Viburnum*) are entirely absent from the cortex. In most of the genera the cork is formed immediately to the inside of the groups of primary bast-fibres, but in a few cases (*Sambucus, Viburnum, Alseuosmia, Carlemannia*) it is produced superficially, either in the epidermis itself or in the outermost cell-layer of the primary cortex. The hairy covering (Fig. 100) consists of the glandular hairs already mentioned (some of these being shortly-stalked capitate hairs, others small peltate glandular hairs), simple, unicellular hairs, and stufted, stellate or peltate hairs. Oxalate of lime is usually only excreted in the form of ordinary solitary and clustered crystals; in *Sambucus* crystal-sand is found; styloids occur in the bast of *Dipelta*. Secretory elements occur only in *Sambucus* where they have the form of long cells, filled with brown, tanniniferous contents.

2. Structure of the Leaf[2]. According to the statements of Vesque and Grignon, the leaves have bifacial structure. In *Triosteum perfoliatum*

[1] With regard to the transference of *Carlemannia* and *Silvianthus* from the Rubiaceae to the Caprifoliaceae on anatomical grounds, see Solereder, Bull. de l'Herb. Boissier 1893.

[2] Most important literature: Vesque, Ann. sc. nat., sér. 7, t. i, 1885, and Solereder, Bull. de l'Herb. Boissier 1893.

and some species of *Viburnum* the palisade-tissue is scarcely developed; on the other hand it is distinctly differentiated in other species of *Viburnum*, in most species of *Lonicera* and in *Leycesteria*. In the species of *Sambucus* and in *Viburnum Opulus*, L. the palisade-parenchyma consists of arm-palisade cells, according to Haberlandt and Loebel. The mesophyll of *Linnaea borealis* is characterized by the presence of large intercellular spaces. The **epidermal cells** almost always have undulated lateral walls. According to Vesque, the nature of the lateral walls in the upper epidermal cells can be employed as a specific character; thus the lateral walls are almost straight in *Leycesteria*, strongly undulated in *Triosteum*, and undulated in a zigzag manner (like the epidermal cells of petals) in *Viburnum Opulus*; the epidermal cells of *Linnaea borealis* have undulated lateral margins provided with marginal pits. The **stomata** are *only found on the lower side of the leaf in most species*; only in the case of *Sambucus nigra* and *S. Ebulus* have a few stomata been observed on the upper side of the leaf in the neighbourhood of the median vein. Special importance attaches to the fact that all the stomata are never accompanied by subsidiary cells parallel to the pore, as is quite generally the case in the Rubiaceae. In all the genera (i.e. in *Abelia*, *Adoxa*, *Alseuosmia*, *Diervilla*, *Dipelta*, *Leycesteria*, *Linnaea*, *Lonicera*, *Pentapyxis*, *Sambucus*, *Symphoricarpus*, *Triosteum*, *Viburnum* and also in *Carlemannia*), with the single exception of *Silvianthus*, the stomata are surrounded by a varying number of epidermal cells exhibiting no regular arrangement or special shape[1]. It may be added that in the same superficial section isolated stomata with subsidiary cells parallel to the pore may sometimes occur side by side with stomata having irregularly arranged neighbouring cells (e.g. in species of *Viburnum*). The guard-cells of the stomata in the genus *Silvianthus*, which is very closely related to *Carlemannia*, are surrounded by at least two subsidiary cells, placed opposite to one another and transversely to the pore. This is the simplest case, but with it a few other modifications occur. Thus in other cases several subsidiary cells, placed transversely to the pore, are found on each side of the pair of guard-cells; or the guard-cells are first surrounded by two subsidiary cells arranged transversely to the pore, as in the simplest case, whilst the group of cells thus formed is enclosed by two further external subsidiary cells, which are parallel to the pore. According to Vesque, the vascular bundles of the **veins** of the leaf are usually (exception: e.g. *Adoxa*) accompanied by groups of sclerenchymatous fibres; occasionally (*Lonicera Standishii*) the latter extend as far as the epidermis on both sides.

Oxalate of lime is chiefly excreted in the form of ordinary solitary and clustered crystals, and occurs in these forms both in the leaf and in the axis. In *Carlemannia* and *Silvianthus* each cell of the palisade-tissue contains a small clustered crystal or a solitary crystal in place of the former, a feature which is highly characteristic of these plants. A noteworthy exception to the general form of the oxalate of lime is presented by the genus *Sambucus*, which is anomalous in other respects also; in this genus crystal-sand occurs. Finally it remains to be mentioned that the bast of *Dipelta floribunda*, Maxim. contains styloids, whilst clustered crystals occur in the parenchyma of the leaf and pith.

The **hairy covering** (Fig. 100) affords valuable anatomical characters. It may in the first place be pointed out once more that, in an investigation

[1] The mode of development of the stomata seems to vary. According to Strasburger (in Pringsheim Jahrb., Bd. v, 1866–7, p. 304 and Tab. xxxvi) the initial cell itself becomes the mother-cell of the pair of guard-cells, and the epidermal cells do not undergo further divisions. Vesque, on the other hand, states that in the development of the stomata several (1–3) divisions precede the formation of the mother-cell of the guard-cells.

carried out in order to amplify Vesque's statements, I have succeeded in demonstrating glandular hairs in all the genera of the Caprifoliaceae, with the exception of the genus *Alseuosmia* (which is also somewhat anomalous in the frequent occurrence of alternate leaves) and of the genus *Adoxa* which is likewise anomalous. These hairs mostly have a spherical or ellipsoidal head, composed of a varying number of cells and borne by a uniseriate stalk of varying length, which is made up of two or more cells; the stalk is in most cases

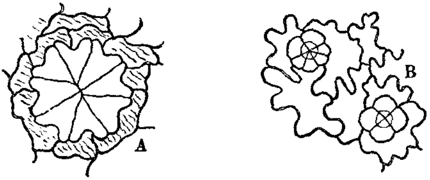

FIG. 100. Hairy covering of the Caprifoliaceae: A, *Viburnum Lentago*, L.; B, *Carlemannia congesta*, Hook. f.—Original.

distinctly marked off from the head, but now and then the demarcation is less distinct. To this category belong the glandular hairs of *Abelia*, *Dipelta*, *Leycesteria*, *Linnaea*, *Lonicera*, *Pentapyxis*, *Sambucus*, *Triosteum* and *Viburnum*. In *Symphoricarpus*, *Carlemannia* (Fig. 100, *B*), *Silvianthus* and *Diervilla* the glandular hairs are peltate; in the first of these genera a small shield of circular outline and consisting of 3–7 cells is seated on the short, unicellular stalk; in *Diervilla*, on the other hand, the shield consists of numerous cells and is constructed like that of the well-known peltate glands of the Oleaceae [1]. Apart from the glandular hairs so far discussed, clothing hairs of various shapes are found in the Order, viz. (*a*) simple unicellular hairs, which vary in length, are mostly pointed, and have a smooth, punctate or striulate surface (*Adoxa*, *Lonicera*, *Sambucus*, *Triosteum*, *Viburnum*); (*b*) the tufted and stellate hairs of certain species of *Viburnum*, which are either directly sunk in the epidermis of the leaf or are provided with a multicellular stalk; and (*c*) the small peltate hairs, occurring in some species of *Viburnum* (*V. pyrifolium* and *V. Lentago*). According to Vesque, the stellate hairs appear to have arisen from the capitate glandular hairs, for the cells of the head of the latter occasionally (e.g. in *Viburnum Opulus*) show a tendency towards ray-formation. The peltate hairs (Fig. 100, *A*) have a shield of 4–8 radially arranged cells, which have approximately the same appearance as the marginal cells in the well-known algal genus *Pediastrum*. We may add, in connexion with the hairy covering, and more especially the glandular hairs, a brief description (based on the work of Reinke and Morini) of the leaf-teeth, which excrete resin and mucilage, and of the peculiar nectarial glands occurring on the petioles (basin-shaped, for example, in *Viburnum Opulus*, flask-shaped in *Sambucus nigra*), or on the rachis of the leaf (*Sambucus Ebulus*), or on the lower margin of the lamina (*Viburnum Tinus*). The leaf-teeth contain the termination of a vein, merging into an epithema, above which a few stomata are situated. The nectarial glands consist of uniform parenchyma, in which a few vascular bundles terminate blindly; palisade parenchyma is wanting.

According to Petit, Vesque, and Grignon, the structure of the **petiole**

[1] Regarding glandular hairs on the buds, see Hanstein, 1868.

and some species [illegible] fibrovascular system is concerned; thus the characteristic [illegible] other [illegible]actéristique') exhibits five isolated vascular bundles in *Sambucus Ebulus*, a ring of vascular bundles with two lateral bundles on its upper side in *Viburnum Tinus*, an arc-shaped vascular bundle in *Lonicera flava*, and a similar bundle with two additional lateral bundles on its upper side in *Viburnum Opulus* and *Leycesteria formosa*.

3. Structure of the Axis[1]. In the structure of the **wood** two features are of primary importance for the anatomical diagnosis[2] of the Order: *the tendency towards the formation of scalariform perforations in the vessels* (exception: *Carlemannia*) and the occurrence of wood-prosenchyma with bordered pits (exceptions: *Sambucus*, *Carlemannia*, and *Alseuosmia*).

The lumina of the vessels vary in size; in *Lonicera japonica* the maximum diameter attains ·1 mm. The wall of the vessel is very commonly provided with spiral thickening; this is the case in all the twenty-one species of *Lonicera* examined by Michael, in *Abelia*, *Leycesteria*, and *Symphoricarpus* according to the same author, and also in *Sambucus peruviana*, H. B. K. (Pomrenke) and *Viburnum Lantana*, L.

Regarding the detailed structure of the perforations of the vessels the following facts may be mentioned. In *Carlemannia* only simple perforations are found; even in the neighbourhood of the primary wood scalariform perforations could not be discovered. In *Sambucus nigra*, L., *S. Sieboldiana*, Bl., and *Lonicera tatarica*, L., all the vessels of the secondary wood are provided with simple perforations of elliptical or circular outline; only in the neighbourhood of the primary wood are scalariform perforations present. *Lonicera Caprifolium*, L., and *Symphoricarpus occidentalis*, Hook., have scalariform perforations in the secondary wood accompanying the simple perforations, some of the former exhibiting a large number of thin bars with narrow slit-shaped perforated areas between them; *Triosteum perfoliatum*, L., for the most part, has scalariform perforations with few bars, simple perforations being very rare. According to my own investigations, exclusively scalariform perforations with a varying number of bars occur in *Viburnum Lantana*, L., and *V. Opulus*, L., in *Linnaea borealis*, L., *Pentapyxis stipulata*, Hook. fil., *Dipelta floribunda*, Maxim., *Alseuosmia linariifolia*, Cunn., and *A. macrophylla*, Cunn. Michael, in his work on the anatomy of the wood in the Caprifoliaceae, also paid attention to the perforations of the vessels, and demonstrated isolated or abundant scalariform perforations in all the 39 investigated species of the genera *Viburnum*, *Diervilla*, *Lonicera*, *Leycesteria*, *Symphoricarpus*, and *Abelia*.

The wood-prosenchyma as a rule bears bordered pits, viz. in the genera *Abelia*, *Diervilla*, *Dipelta*, *Leycesteria*, *Linnaea*, *Lonicera*, *Pentapyxis*, *Symphoricarpus*, *Triosteum*, and *Viburnum*. In addition to the bordered pits spiral thickening of the wall of the prosenchymatous cells is found in certain species of *Abelia*, *Leycesteria*, *Lonicera*, *Symphoricarpus*, and *Viburnum*. Unlike that of the ten genera named above, the wood-prosenchyma bears simple pits in the genera *Sambucus*, *Alseuosmia*, and *Carlemannia*, and in the last two of these it is commonly provided with delicate transverse walls. A transition to this type of wood-prosenchyma is afforded by *Leycesteria formosa*, in which, according to Michael, wood-fibres with simple pits occur side by side with wood-prosenchyma having bordered pits, the latter being abundantly developed. The wood-parenchyma is not strongly developed. The medullary rays of the wood vary in breadth; in species of *Lonicera* and *Symphoricarpus*, for example, they are 8–10, in *Abelia* only 1–3 cells broad. According to Michael, the structure of the medullary rays in tangential longitudinal section is characteristic, so that from this point of view a predominant type can be established for the Order; this type is only wanting in *Sambucus*

[1] Most important literature: Solereder, Holzstr., 1885, and Bull. de l'Herb. Boissier, 1893; Möller, Rindenanat., 1882.

[2] The structure of the branch of *Silvianthus* has not been examined.

amongst the genera investigated by Michael and those subsequently investigated by Linsbauer (these do not, bowever, include all the genera). The middle of the medullary ray in a tangential section is occupied by low cells, above and below which cells of medium size are to be found; finally at the upper and lower end of the ray high cells occur. Other types, it is true, are found also, but they can readily be derived from the main type just described by supposing one or other kind of cell (but never all the high cells) to be suppressed. In *Sambucus* alone the elongated cells of the medullary rays are entirely wanting.

I will now describe the structure of the **cortex**, and in the first place the mode of development of the cork. In most cases the cork arises deep down in the interior of the cortex, immediately internal to the groups of primary bast-fibres, i.e. in the pericycle; it is rarely developed superficially. Superficial cork-formation is characteristic of the genera *Sambucus*, *Viburnum*, *Alseuosmia*, and *Carlemannia*; in some of the species of *Viburnum* (e.g. *V. Lantana*, L., *V. Lentago*, L., &c.) the epidermis becomes the phellogen; in other species of *Viburnum* (e.g. *V. americanum*, Mill., *V. Opulus*, L., &c.), in *Sambucus*, *Alseuosmia*, and *Carlemannia* on the other hand the phellogen is derived from the outermost cell-layer of the primary cortex. Development of cork in the pericycle has been observed by various authors (Möller, Douliot, J. E. Weiss, Solereder) in the genera *Abelia*, *Diervilla*, *Dipelta*, *Leycesteria*, *Linnaea*, *Lonicera*, *Symphoricarpus*, and *Triosteum*. From these enumerations it is evident that pericyclic development of cork does not occur in all the members of the tribe Lonicereae. According to the statements of Möller and J. E. Weiss with reference to *Abelia*, *Diervilla*, *Lonicera*, *Sambucus*, *Symphoricarpus*, and *Viburnum*, the cork-cells generally speaking have wide lumina, and either thin or thick walls. The primary cortex contains typical collenchyma in *Sambucus* and *Viburnum*. In the primary cortex of the plants examined by Möller (*Diervilla*, *Lonicera*, *Sambucus*, *Symphoricarpus*, *Viburnum*) sclerosis does not occur. The pericycle in almost all cases contains bast-fibres or cells like bast-fibres, which moreover vary in structure, occasionally having very wide lumina, and either forming groups of varying extent or uniting to form a ring; a composite and continuous sclerenchymatous ring has only been recorded in *Viburnum foetens*, Decne. Secondary hard bast, sometimes showing concentric differentiation, has been observed by Möller in the cortex of species of *Lonicera*, *Symphoricarpus*, and *Sambucus*, but not in *Viburnum*, where it is replaced by groups of stone-cells.

According to Gris, the **pith** is heterogeneous in *Abelia*, *Diervilla*, *Lonicera*, and *Symphoricarpus*; it is composed of dead cells in *Sambucus*. In some of the species of *Lonicera*, such as *L. Caprifolium* or *L. Xylosteum*, the internal portion of the pith of the internode is absorbed at an early stage.

A special structural feature consists in the girdle-shaped commissural strands found in the nodes of the stem; they are said to occur only in *Sambucus* (Hanstein, Fritsch). Mention has already been made (see structure of the leaf) of the crystals in the axis, but we have still to discuss the **secretory sacs**, which are situated in the peripheral part of the pith and in the pericycle of *Sambucus*, and have brown, homogeneous and gelatinous, tanniniferous contents. According to Linsbauer, they occur quite generally in the genus *Sambucus*. They have long been known in *S. nigra* and *S. Ebulus*; Linsbauer enumerates the following additional species: *S. Gautschii*, Wetts., *S. glauca*, Nutt., *S. pubens*, Michx., *S. racemosa*, L. and *S. Thunbergiana*, Bl. (in part contrary to Fritsch's statements).

Note.—The 'réseau de soutien' of Van Tieghem is met with in the root of many members of the Order, in the cell-layer situated immediately internal to the endodermis; thus, according to Van Tieghem, it occurs in the genera *Viburnum*, *Lonicera*,

Symphoricarpus, Leycesteria, Diervilla, and *Triosteum,* but not in *Sambucus, Abelia,* and *Linnaea.* Its differentiation varies even within the genus *Viburnum.* For details see Van Tieghem, loc. cit.

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RUBIACEAE.

1. Review of the Anatomical Features. This Order is already characterized by certain exomorphic features, which can be recognized even in sterile material, viz. opposite leaves, in which the margin is almost invariably entire, as well as stipular structures, which are scarcely ever wanting, and are peculiar in their position and cohesion (or are leaf-like in the Stellatae). In addition to these external characters, however, there are certain features belonging to the internal structure, which may be of critical value for the recognition of sterile material of a member of the Order: 1. The stomata are invariably accompanied by subsidiary cells, arranged parallel to the pore (Fig. 101, *D–G*). (2) Glandular hairs, which are very abundant in the closely-allied Caprifoliaceae, are not present on the leaves of the Rubiaceae. (3) The vascular bundles of the axis are simply collateral (not bicollateral).

With regard to the general structure of the axis, it may be mentioned that the formation of cork may be superficial or internal, that the perforations of the vessels are generally simple, scalariform perforations only occurring rarely and always in relatively small numbers, and that the wood-prosenchyma in the majority of the genera investigated has bordered pitting only, simple pits occurring in the remainder of the genera, in which also the prosenchyma is occasionally provided with delicate transverse walls. The following secretory elements occur: Glandular shaggy hairs on the stipules (Fig. 101, *A*), schizogenous secretory cavities (*Rustia, Tresanthera*), epidermal cells with a resinous secretion (species of *Rubia, Nenax,* and *Anthospermum*), resin-cells in the mesophyll (*Polysphaeria*), secretory cells, filled with brown contents (*Phyllis, Randia,* &c.), elongated secretory sacs (*Cinchona, Henriquezia, Casca-*

rilla, Isertia, Ladenbergia, Mussaenda, Remijia), and internal glands, formed by a group of secretory cells (*Heterophyllaea*). Oxalate of lime is only in exceptional cases secreted in the form of ordinary large rhombohedra. Elsewhere it is found in various forms, namely, as clustered crystals, crystal-sand, small acicular crystals, raphides and styloids. The different forms assumed by the excreted oxalate of lime are characteristic of certain tribes or genera. The hairy covering generally consists of simple, unicellular or uniseriate hairs; in *Isertia* tufted hairs occur. A very characteristic feature of the tribe Guetardeae is afforded by the crystal-hairs ('Krystallhaare'), i.e. unicellular hairs, in the thick walls of which small rhombohedral crystals are deposited in linear series (see Fig. 101, *B–C*). A few additional anatomical features, which are useful for detailed diagnosis, are as follows: the occurrence of a hypoderm in the leaf; the presence of sclerenchymatous fibres and of spiral tracheids in the mesophyll; the arrangement of the stomata in groups (*Pagamea*); crystal-sclerenchyma (*Webera, Pavetta, Strumpfia*); the rod-cells of the true China bark; the furrowed xylem-mass in some lianes (*Lygodysodea, Manettia, Sabicea*); the occurrence of small strands of wood and bast in the primary cortex (*Chiococca racemosa*, Jacq., Fig. 102).

2. Structure of the Leaf. The ordinary features in the leaf-structure, such as its general differentiation and the nature of the epidermis, have only been examined in a few species. The following statements can therefore only serve as a preliminary general account of this subject. The leaf-structure is bifacial in the cases investigated, as for example in all the species of *Gaertnera* and *Chasalia* examined by me. The **epidermal cells** have straight or undulated lateral walls; the marking of the cuticle varies. Marginal pits ('Randtüpfel') have been observed in *Remijia pedunculata*; papillose differentiation of the upper epidermis has been found in *Psychotria egensis*, and the same character in the lower epidermis in *Pagamea plicata*, Spruce. Gelatinization of the epidermis of the leaf has not hitherto been observed in any member of the Order; on the other hand, **hypoderm** is developed in *Cinchona succirubra, Calisaya, Condaminea*, and *Coprosma Baueri*, according to Vesque; in *Scyphiphora hydrophyllacea*, Gaertn. f., according to Schimper, in certain epiphytic species of *Psychotria*, according to Johow, in *Rustia formosa*, Klotzsch, and numerous species of *Gaertnera, Chasalia*, and *Pagamea* (see Solereder, Gaertnereen, 1890), according to my own investigation. *Gaertnera truncata*, DC., and *G. Walkeri*, Wight, show no more than a tendency to form a hypoderm, i.e. in these species some only of the epidermal cells are divided by thick septa, parallel to the surface of the leaf.

The **stomata** are mostly only to be found on the lower side of the leaves. In all the genera (to be enumerated later in the discussion of the features exhibited by the crystals) the stomata are invariably accompanied by two or more subsidiary cells, placed parallel to the pore. The number of these subsidiary cells and their mode of attachment to the guard-cells varies according to the genus or species (Fig. 101, *D–G*). In some cases only a simple subsidiary cell is found on each side of the pair of guard-cells. In other cases two or more parallel subsidiary cells are arranged on one or both sides of the guard-cells. The mode of attachment may be of two kinds in each case: (*a*) the subsidiary cells do not envelop one another in surface-view, being simply arranged parallel to the guard-cells and to one another, when more than two subsidiary cells are present; or (*b*) they partly envelop one another, and in this case, if more than two subsidiary cells are formed, the cell situated to the right of the pore is seen in surface-view to be enveloped by one on the left, this again by one on the right and so on. In the genus *Pagamea* the stomata are not, as in other cases, scattered over the entire lower side of the leaf, but are united in varying numbers (2–4) to form stomatal groups. These latter can be detected occasion-

ally as circumscribed areas even with the naked eye or with the help of a lens, and they occur in all the species of *Pagamea* investigated; in *P. coriacea*, Spruce, and *P. plicata*, Spruce, they are depressed below the level of the epidermis.

The appearance of sclerenchymatous fibres or of curious spirally thickened tracheides in the tissue of the leaf is a special feature, which may now be described. The fibres were first observed by Vesque in *Burchellia bubalina* and by myself in *Chomelia Martiana*, Müll. Arg.; they traverse the mesophyll in all directions, and in *Burchellia* penetrate between the epidermal cells, occasionally even

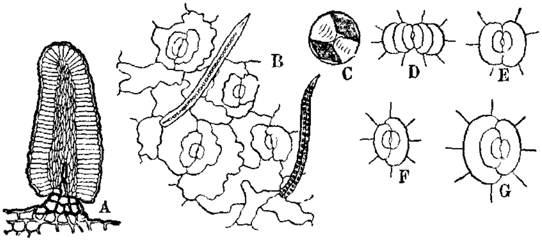

FIG. 101. A, Glandular shaggy hair of *Isertia coccinea*, Vahl. B, C, Crystal-hairs on the lower side of the leaf of *Malanea macrophylla*, Bartl.; C, crystal-hair in transverse section. D–G, Types of stomata.—Original.

as far as the cuticle, which is sometimes slightly elevated in consequence. I have demonstrated the spirally thickened tracheides in the genera *Sommera*, *Chomelia*, *Macrocnemum* and *Pentagonia*.

The meshes of the network, formed by the veins of the leaf in *Sommera sabiceoides*, K. Schum., are marked by parallel transverse lines, which are differently orientated in each mesh. These transverse lines are formed by delicate veins, above the xylem of which one finds a group of tracheid-like, spirally thickened prosenchymatous cells with rather wide lumina, which do not however belong to the wood; these cells certainly play a part in the maintenance of the water-supply. They are evidently homologous with the sclerenchyma, which elsewhere, as is well known, very frequently accompanies the vascular bundles of the veins of the leaf above and below. The spiral band consists of several parallel strips of thickened wall, i.e. it is not simple, as in the spiral vessels of the bundles.

Similar transverse lines are found in the leaves of *Chomelia Pohliana*, Müll. Arg. The vascular bundles of the veins, which give rise to them, however, only contain sclerenchymatous fibres with thick walls and narrow lumina above the xylem; only in their possession of a distinct spiral striation do these fibres recall the above-described tracheide-sclerenchyma of *Sommera*.

The genus *Macrocnemum* (*M. cinchonoides*, Wedd., *M. glabrescens*, K. Schum., and *M. roseum*, Wedd.) has tracheides of a special kind. The veins are here connected by parallel elongated tracheides having a very wide lumen and thin walls; the tracheides are pointed at the ends (which are devoid of perforations), and are provided with a simple, very closely wound spiral band. Towards the under side of the leaf a small group of soft bast or a little sclerenchyma may adjoin these tracheides; and occasionally they are surrounded by a sheath of small parenchymatous cells with thin walls. The tracheides in question may sometimes give rise to transparent lines on the dried leaf.

A very peculiar marking, which is likewise due to tracheides, is shown by the lower surface of the leaf of *Pentagonia spathicalyx*, K. Schum. The lateral veins of the first order are connected by numerous transverse veins of variable size, running at right angles to them. These transverse veins are intersected at an acute angle by a system of striae, consisting of bundles of tracheides

which have the same structure as those of *Sommera,* their walls being thin, the lumina not especially wide and the spiral band composite. They lie close to the epidermis on the lower side of the leaf, and hence the system of striae is noticeable on that side alone in leaves which exceed a certain thickness. Exactly similar tracheides occur above the xylem of the vascular bundles in the veins of the leaf, that is to say, in the same position as in *Sommera.*

Features in the venation similar to those in the genera just referred to occur in *Stilpnophyllum, Tammsia, Hippotis,* and *Pauridiantha,* according to the statements of systematists. It remains to be determined by future investigation whether tracheides are concerned in these cases.

With regard to the **hairy covering**, it may first be pointed out that, contrary to what is shown by the closely allied Caprifoliaceae, glandular hairs are entirely wanting on the foliage leaves of the Rubiaceae. It is only on the stipules that external glands frequently occur in the form of glandular shaggy hairs. Their mucilaginous and resinous secretion is frequently so abundant that not only are the young leaves, emerging from the stipular sheath, coated with resin (as a protection against desiccation) but even the older leaves retain this coating and appear as though they were varnished. The glandular shaggy hairs in question mostly occur on the inner surface of the stipules. In those species in which the stipules are subdivided into bristle-like segments, the tips of the bristles are transformed into glandular shaggy hairs (*Coprosma Baueriana*, according to Gardiner, *Pentas lanceolata,* K. Sch. and *P. Schimperiana*, Vatke). The structure of these glands is in all cases the same (Fig. 101, *A*). The central core of the ellipsoidal body of the gland is composed of a strand of several rows of elongated cells, which passes over into the short multiseriate stalk below, and is surrounded on all sides by a layer of palisade-like cells, placed perpendicularly to the central strand; the secretion is subcuticular in origin.

The forms of clothing hair are unicellular and uniseriate simple hairs and tufted hairs (the latter in *Isertia*). The unicellular hairs are often characterized by extreme shortness; as in *Bouvardia cordifolia,* where each epidermal cell of the upper side of the leaf is produced into a short hair, and in *Psychotria egensis,* and *Rustia formosa,* Kl., where they are sunk in pits on the leaf-surface, from which they scarcely project. *Randia tetrasperma* is an example of a species possessing long unicellular trichomes. The uniseriate hairs vary in the nature of their walls and tips, and in the number and length of their component cells. The pointed hairs of *Mussaenda Roxburghii,* Hook. f., for example, have a thick external wall and thin septa; the articulated hairs of *Oldenlandia japonica,* Miq. are composed of rather long cells, those of *Argostemma sarmentosum,* Wall. of short and rounded elements. Among special forms of simple unicellular hairs are hairs which are curved like a hook at the tip; these occur in *Randia,* according to Vesque, and play a part in the formation of the prickles on the leaf-margin and on the ribs of the stem in species of *Asperula* and *Galium*; also, secondly, the crystal-hairs of the Guettardeae. The latter are simple unicellular, thick-walled trichomes with narrow or almost obliterated lumina; in the cell-wall of these hairs numerous small rhombohedral crystals of oxalate of lime are embedded in longitudinal rows. Such hairs are found in all Guettardeae[1] which possess any hairy covering at all, and accompany ordinary unicellular hairs, devoid of crystals. If we follow their development we find that the crystals first originate freely in the protoplasm, where they gradually attain the size that they have in the fully-developed hair; subsequently by the rather sudden appearance of one or two longitudinal strips of thickening they assume a linear arrangement and become included in the cell-wall.

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[1] They have been observed in the genera *Guettarda, Antirrhaea, Rhytidotus, Bobea, Timonius, Chomelia,* Jacq. (= *Anisomeris,* Presl.), *Malanea* and *Laugeria*; not, however, in *Abbotia* (= *Timonius* sp.) and *Machaonia.*

The **internal glands** occurring in this Order are schizogenous secretory cavities, secretory cells of diverse shapes and with various contents, and peculiar glands formed by a group of secretory cells.

Schizogenous secretory cavities, filled with a resinous secretion, characterize the very closely-related genera *Rustia* and *Tresanthera*, and generally give rise to transparent dots in the leaf.

Amongst the secretory cells, those may be mentioned first which are not elongated in the form of tubes. In herbarium material, these elements either possess resinous or brown tanniniferous contents, and mostly also contain mucilage. The resiniferous secretory cells include the following forms: the large secretory cells, discovered by Radlkofer in the lower epidermis of the leaf in certain species of *Rubia* (*R. indecora*, Ch. et Schl., *R. valantoides*, Ch. et Schl., *R. Relbun*, Ch. et Schl.), and giving rise to pellucid dots; the secretory cells in the lower epidermis of all species of *Anthospermum* examined by me; the secretory cells of the upper epidermis of *Nenax rosea*, Gaertn.; finally, secretory cells having wide lumina in the mesophyll of *Polysphaeria parvifolia*, Hiern (Stuhlmann, No. 7002), quite recently observed by me. Secretory cells, filled with brown contents, are found: (*a*) firstly in the leaf of *Phyllis*, where they generally have the form of branched cells, which are frequently united into groups or series; (*b*) in the mesophyll of *Randia aculeata*, L., where they form a middle layer in the leaf and also occur as dilated cells in the palisade-tissue; (*c*) similarly in the leaf of *Plectronia ventosa*, L. and *Vangueria edulis*, Vahl, and, according to Vesque, also in the leaf of *Gardenia Stanleyana* in the form of enlarged cells of the palisade-tissue; (*d*) finally in the bast of *Cascarilla magnifolia*, Wedd., *Vangueria edulis*, Vahl, and *Fadogia ancylantha*, Schweinf. Their distribution in the Order will probably prove to be a rather wide one. The mucilage-containing cells in the mesophyll of *Pentanisia variabilis*, Harv., and *Holocarpa veronicoides*, Bak. may be classed amongst the short secretory cells (those which are not developed in tubular form); they may possibly be regarded as reduced raphide-sacs (raphide-cells, devoid of raphides). Elongated secretory sacs have been observed in *Mussaenda*, *Isertia*, *Cinchona*, *Cascarilla*, *Remijia*, *Ladenbergia*, and *Henriquezia*. In the species of *Mussaenda* they are found both in the veins of the leaf, accompanying the vascular bundles, and also in the pericycle of the axis; in the latter they occur in the form of long cells, reaching 1 cm. in length, similar to hard bast-fibres. In *Henriquezia* they have so far only been investigated in the petiole, in which they occur in groups external to the hard bast. The secretory sacs of the remaining genera usually occur in the pericycle of the axis, more rarely scattered in the primary cortex. In *Cinchona* they have also been shown to occur in the petiole and veins of the leaf (Koch). Their length is often very considerable, as for instance in *Cinchona*, where the secretory sacs were formerly described as laticiferous vessels, and are as long as an entire internode, according to Koch; they generally terminate prosenchymatously in the nodes. Their contents in the dry bark form a yellowish to reddish-brown, glassy or friable mass, often containing tannin; in the living plant—at all events, in the species of *Cinchona*—the contents are of the nature of latex, according to the concordant statements of various observers. The distribution of the secretory sacs in the genera mentioned requires further examination from a systematic point of view; as far as *Cinchona* is concerned, the secretory sacs are found[1] in all species of Linnaeus's genus (perhaps with the exclusion of *C. hirsuta*, R. et P.), according to Karsten.

The above-mentioned peculiar internal glands, occurring in *Heterophyllaea pustulata*, Hook. f., are spherical groups of thin-walled cells, the brown contents

[1] Concerning the distribution of the secretory sacs in *Cinchona* see also Vogl, 1867; with regard to *Remijia* see Planchon, 1884.

of which dissolve in alkalis, the solution having a carmine-red coloration; the glands are delimited from the remainder of the leaf-tissue by layers of cells resembling an epithelium. They constitute the verrucose prominences on the branches, on the leaf-surface and in the angles of the crenate teeth of the leaf-margin.

In connexion with the description of the secretory organs the frequent occurrence of fat-bodies in the assimilatory tissue of the dry leaf may be mentioned.

The mode of excretion of **oxalate of lime** is of special value for the diagnosis of the genera and tribes in this Order. In this connexion it may be especially noticed that the large rhombohedral crystals which, as is well known, are abundant in many Orders, have only been observed in very rare cases in the Rubiaceae (cortex of *Basanacantha spinosa*, K. Sch., phloem of species of *Pavetta*, veins of the leaf of *Gardenia Thunbergia*, L. f.). Small rhombohedral crystals are found in the crystal-hairs of the Guettardeae, already discussed above, and in the crystal-sclerenchyma of *Pavetta, Strumpfia,* and *Webera,* which will be described in detail under the structure of the cortex. In addition to this, oxalate of lime occurs in the form of raphides, styloids, crystal-sand, clustered crystals and small acicular crystals. The elements in which the raphides are contained are frequently very long sausage-shaped cells, especially those in the mesophyll. Generally the sacs with raphides also contain mucilage, especially the much-elongated sacs, which occasionally (*Knoxia corymbosa,* Willd.) are several times as long as the enclosed raphide-bundles. Very short raphides occur in the epidermis of *Aphiorhiza eriantha,* Wight. Occasionally the needles are of considerable thickness, so that they constitute a transition to styloids. The bundles of raphides rarely (*Dirichletia insignis,* Vatke, *Manettia Lygistum,* Sw. and species of *Otomeria*) give rise to transparent dots or fine striae. In numerous genera styloids appear in place of raphides or accompany them. The styloids rarely occur side by side with clustered crystals in the absence of raphides. The long axis of the styloids is occasionally (species of *Palicourea*) placed in the direction of that of the palisade-cells of the leaf, and if the latter is sufficiently thin the styloids give rise to very fine transparent dots and a roughness of the leaf-surface, the latter character being perceptible to the touch. The sacs containing **crystal-sand** are occasionally recognizable by the naked eye as bright dots on the surface of the leaf, or by their white powdery contents in the cortex of a transverse section of the branch; it should be mentioned that in a few rare cases (*Chione glabra,* DC.) the crystal-sand occurs in the epidermis of the leaf, and that occasionally, when absent in the leaf, it is to be found in the axis of the same species. The branched sacs, containing crystal-sand, in the leaf of *Amaralia* and *Bertiera* deserve special notice. The clustered crystals vary in size and shape. Occasionally crystal-sand is found in the same cell with a clustered crystal, as in *Sarcocephalus Russeggeri,* Kotschy. The clustered crystals of *Stephegyne* have sphaerocrystalline structure. The occurrence of small acicular crystals in the leaf-tissue together with oxalate of lime in one or other of its forms of excretion is not rare; as examples, *Mussaenda, Plectronia* and *Randia* may be mentioned.

In the following I first give a review of the mode of excretion of oxalate of lime in the several tribes of the Order (according to the system of Bentham and Hooker); for the particulars of the material on which this investigation was based, see Solereder, 1893.

Tribe I. Naucleae: Crystal-sand, occasionally together with clustered crystals.

Tribe II. Cinchoneae: Crystal-sand in most genera. Raphides in *Bouvardia, Heterophyllaea, Hindsia, Hymenopogon, Manettia,* and *Danais,* in *Hillia* and *Coptosapelta.* Clustered crystals and styloids (the latter in the bast) in *Crossopteryx.*

Tribe III. Henriquezieae: Crystal-sand in *Henriquezia*.

Tribe IV. Condamineae: Crystal-sand, occasionally together with clustered crystals.

Tribe V. Rondeletieae: Mostly crystal-sand. Clustered crystals alone in *Greenea*; raphides in *Deppea*; no crystalline elements in *Limnosipanea*.

Tribe VI. Hedyotideae: Raphides, occasionally together with clustered crystals (with the exception of the genera *Carlemannia* and *Silvianthus*, which have been transferred to the Caprifoliaceae).

Tribe VII. Mussaendeae: Crystal-sand in *Mussaenda*, *Gonzalea*, *Sabicea*; raphides in *Schradera*, *Adenosacme*, *Myrioneuron*, *Urophyllum*, *Coccocypselum*, *Lecananthus*; clustered crystals in *Isertia*.

Tribe VIII. Hamelieae: Raphides in *Hamelia* and *Hoffmannia*; crystal-sand in *Bertiera*, *Bothryospora*, and *Heinsia*.

Tribe IX. Catesbaeeae: Crystal-sand in *Pentagonia* and *Sommera*; clustered crystals in *Catesbaea*.

Tribe X. Gardenieae: Mostly crystal-sand, occasionally together with clustered crystals. Clustered crystals alone in *Morelia* and *Sphinctanthus*. Occasionally also solitary crystals (in species of *Basanacantha* and *Gardenia* and in the crystal-sclerenchyma of the genus *Webera*, which approximates more to the Ixoreae).

Tribe XI. Cruckshanskieae: Raphides in *Cruckshanskia*.

Tribe XII. Retiniphylleae: Crystal-sand in *Jackia*; no crystalline elements in *Retiniphyllum*.

Tribe XIII. Guettardeae: Crystal-sand, occasionally together with clustered crystals. (In addition to these, small solitary crystals in the crystal-hairs, see above.)

Tribe XIV. Knoxieae: Raphides in *Knoxia* and *Pentanisia*.

Tribe XV. Chiococceae: Crystal-sand in *Chiococca*, *Erithalis*, *Chione*, and *Scolosanthus*.

Tribe XVI. Alberteae: Crystal-sand in *Alberta*, *Polysphaeria*, *Rhabdostigma* (with *R. Kirkii*, Hiern), and *Nematostylis*; small acicular crystals in *Aulacocalyx jasminiflora*, Hook. f.

Tribe XVII. Vanguerieae: Clustered crystals and small needles in *Plectronia*, *Fadogia*, and *Vangueria*.

Tribe XVIII. Ixoreae: Crystal-sand in *Pavetta* and *Coffea*, sand and clustered crystals in *Strumpfia*; clustered crystals and styloids in *Myonyma* and *Ixora*. (Further, solitary crystals in the sclerenchyma of *Pavetta* and *Strumpfia*.)

Tribe XIX. Morindeae: Raphides in *Morinda* and *Damnacanthus*.

Tribe XX. Coussareae: Raphides.

Tribe XXI. Psychotrieae: Raphides, occasionally together with styloids.

Tribe XXII. Paederieae: Raphides in *Paederia*, *Hamiltonia*, *Leptodermis*; in *Paederia* styloids also.

Tribe XXIII. Anthospermeae: Raphides.

Tribe XXIV. Spermacoceae: Raphides, occasionally together with clustered crystals.

Tribe XXV. Galieae: Raphides.

To this first synopsis a second is added, which shows in which genera the various modes of crystal-excretion are found. Under each mode of occurrence the genera are arranged in alphabetical order. It may be added that, according to my experience, in the case of the genera mentioned under 'sand and clustered crystals,' and likewise in the case of those mentioned under 'raphides and clustered crystals,' the crystal-sand and raphides respectively constitute the characteristic feature. It may happen that, in one or other of the species of the genera mentioned under 'sand and clustered crystals' or 'raphides and clustered crystals,' the clustered crystals may be wanting, and conversely that clustered crystals may be present in species of the genera mentioned as having sand or raphides only:

I. Crystal-sand (i.e. crystal-sand alone or together with clustered crystals) is found in the following genera: *Adina*, *Alberta*, *Alibertia*, *Alseis*, *Amajoua*, *Amaralia*, *Anthocephalus*, *Antirrhoea*, *Basanacantha*, *Bathysa*, *Bertiera*, *Bikkia*, *Bobea*, *Bothryospora*, *Burchellia*, *Calycophyllum*, *Cascarilla*, *Cephalanthus*, *Chimarrhis*, *Chiococca*, *Chione*, *Chomelia*, *Cinchona*, *Coffea*, *Condaminea*, *Coutarea*, *Diplospora*, *Dolicholobium*, *Duroia*, *Erithalis*, *Elattospermum*, *Exostemma*, *Ferdinandusa*, *Feretia*, *Fernelia*, *Galiniera*, *Genipa*, *Gonzalea*, *Guettarda*, *Heinsia*, *Henriquezia*, *Hymenodictyon*, *Hyptianthera*, *Jackia*, *Ladenbergia*, *Laugeria*, *Luculia*, *Machaonia*, *Macrocnemum*, *Malanea*, *Mitriostigma*, *Molopanthera*, *Mussaenda*, *Mussaendopsis*, *Nauclea*, *Nematostylis*,

Pavetta, Pentagonia, Petunga, Pinkneya, Pognopus, Polysphaeria, Portlandia, Posoqueria, Remijia, Rhabdostigma, Rhytidotus, Rondeletia, Rustia, Sabicea, Sarcocephalus, Scolosanthus, Sichingia, Sipanea, Sommera, Stephegyne, Strumpfia, Timonius, Tocoyena, Tricalysia, Uncaria, Villaria, Warscewiczia, Webera, Wendlandia, Zuccarinia.

Together with the crystal-sand, clustered crystals were also observed in: *Alibertia, Amajoua, Basanacantha, Bobea, Chimarrhis, Duroia, Genipa, Hymenodictyon, Nauclea, Pogonopus, Portlandia, Rhytidotus. Sabicea, Sarcocephalus, Stephegyne, Strumpfia, Uncaria.*

II. Raphides (i.e. raphides alone or together with clustered crystals or styloids) occur in the following genera: *Adenosacme, Anthospermum, Argostemma, Asperula, Bouvardia, Callipeltis, Carpacoce, Chasalia, Coccocypselum, Coptosapelta, Coussarea, Crucianella, Cruckshanskia, Crusea, Damnacanthus, Danais, Declieuxia, Dentella, Deppea, Diodon, Dirichletia, Emmeorhiza, Ernodea, Faramea, Gaertnera, Gaillonia, Galium, Galopina, Hamelia, Hamiltonia, Hedyotis, Hemidiodia, Heterophyllaea, Hillia, Hindsia, Hoffmannia, Holocarpa, Houstonia, Hydrophylax, Hymenopogon, Karamischewia, Kellogia, Knoxia, Lasianthus, Lecananthus, Leptodermis, Manettia, Mapouria, Mericarpaea, Mitchella, Mitracarpum, Morinda, Myrioneuron, Nenax, Nertera, Octodon, Oldenlandia, Ophiorhiza, Otiophora, Otomeria, Paederia, Pagamea, Palicourea, Pentanisia, Pentas, Pentodon, Perama, Phyllis, Plocama, Polyura, Pomax, Psychotria, Psyllocarpus, Putoria, Relbunium, Richardsonia, Rubia, Rudgea, Saprosma, Schradera, Serissa, Sherardia, Spermacoce, Spiradiclis, Staelia, Triodon, Urophyllum, Vaillantia.*

In addition to the raphides, clustered crystals occur in: *Bouvardia, Crusea, Diodia, Emmeorhiza, Ernodea, Hemidiodia, Lecananthus, Oldenlandia, Schradera, Spermacoce, Triodon.*

Styloids are found side by side with the raphides in: *Adenosacme, Mapouria, Paederia, Palicourea, Psychotria.*

III. Clustered crystals alone or together with small acicular crystals or styloids, but not with raphides (see under II) or crystal-sand (see under I), are found in: *Catesbaea, Crossopteryx, Fadogia, Gardenia, Greenea, Isertia, Ixora, Morelia, Myonyma, Plectronia, Randia, Sphinctanthus, Vangueria.*

Clustered crystals and styloids occur in *Crossopteryx, Ixora, Myonyma.*

IV. Small acicular crystals occurring alone or together with another crystal form (sand, raphides, or clustered crystals) have come under my notice in the following: *Aulacocalyx, Chasalia, Fadogia, Gaertnera, Lecananthus, Mussaenda, Plectronia, Randia. Schradera, Vangueria.*

V. With regard to the occurrence of solitary crystals and styloids the details have been already mentioned above.

VI I have been unable to observe any crystalline elements in *Limnosipanea* and *Retiniphyllum.*

In connexion with the discussion of the crystalline elements it may be mentioned that cystoliths are absent. Haeckel's statement as to their occurrence in *Exostemma* is incorrect.

3. Structure of the Axis. The structure of the axis has as yet been little investigated in proportion to the size of the Order, so that the following remarks can only have the value of a preliminary review.

With regard to the structure of the **wood**, the essential data given in my 'Holzstruktur,' and based on the investigation of forty-one species, belonging to the various tribes[1], and on Michael's work, may be repeated. Every anatomical character shows itself to be variable within the limits of this large Order. The vessels vary in their arrangement and in the size of their

[1] The genera in question are: *Nauclea, Uncaria* (Naucleae); *Cinchona, Cascarilla* (Cinchoneae); *Bikkia, Portlandia* (Condamineae); *Rondeletia, Wendlandia* (Rondeletieae); *Hedyotis* (Hedyotideae); *Urophyllum* (Mussaendeae); *Hamelia* (Hamelieae); *Catesbaea* (Catesbaeeae); *Gardenia, Discospermum* (Gardenieae); *Retiniphyllum* (Retiniphylleae); *Antirrhoea, Guettarda* (Guettardeae); *Knoxia* (Knoxieae); *Chiococca, Scolosanthus* (Chiococceae); *Vangueria, Pachystigma* (Vanguerieae); *Ixora, Coffea* (Ixoreae); *Morinda, Damnacanthus* (Morindeae); *Coussarea, Faramea* (Coussareae); *Psychotria, Lasianthus, Rudgea* (Psychotrieae); *Paederia, Leptodermis, Hamiltonia* (Paederieae); *Anthospermum, Nenax* (Anthospermeae); *Gaillonia, Psyllocarpus* (Spermacoceae).

lumina; the latter is as much as ·075 mm. in *Guettarda viburnoides*, Ch. et Schl., for example; in *Nauclea Cadamba*, Roxb. it is as much as ·054 mm., in *Cascarilla magnifolia*, Wedd. it reaches ·045 mm., in *Hedyotis articularis*, R. Br. ·03 mm., and in *Scolosanthus triacanthus*, DC. ·024 mm. In the vessels the size of the border of the pits varies from ·0017 to ·004 mm. A delicate spiral thickening of the vessel-wall is frequently found, e.g. in *Vangueria infausta*, Burch. Where in contact with ray-parenchyma the vessel-wall is provided with bordered pits. The perforations of the vessels are generally simple throughout, and circular or elliptical in shape (elongated-elliptical in *Urophyllum longifolium*, Wight). Side by side with the simple perforations, scalariform openings occur in a large number of the species[1] investigated; they usually have few bars and are confined to the neighbourhood of the primary wood. Perforations with numerous thin bars and narrow openings have been observed in *Psychotria jambosioides*, Schlecht. and species of *Gaertnera*. The occurrence of scalariform and simple perforations side by side is sometimes characteristic of all the species of a genus (as in *Gaertnera* and *Pagamea*, but not in *Chasalia*[2]). The medullary rays are uniseriate to quadriseriate in branches from herbarium-material; Michael mentions 8-seriate rays in the ten-year-old wood of the stem of *Coprosma lucidum*. The ray-cells are frequently distinguished by their considerable height. The wood-parenchyma is often but slightly developed; it is abundant in the species of *Urophyllum*, *Morinda*, and *Retinophyllum* examined by me. The wood-prosenchyma bears either bordered or simple pits. Typical prosenchyma with bordered pitting occurs in the investigated members of the tribes Naucleae, Cinchoneae, Condamineae, Rondeletieae, Hedyotideae, Mussaendeae, Gardenieae, Retiniphylleae, Chiococceae, Knoxieae, Alberteae, Vanguerieae, Ixoreae, and Anthospermeae, in *Psyllocarpus* among the Spermacoceae, and in *Lasianthus*, *Gaertnera*, and *Pagamea* among the Psychotrieae. In the remaining genera[3] examined, the pitting of the wood-prosenchyma is simple, or at any rate only small indistinct pit-borders are to be found. The simple-pitted prosenchyma is occasionally divided up by thin partition-walls, as in species of *Damnacanthus*, *Guettarda*, *Hamelia*, *Psychotria*, *Chasalia*, *Rudgea*, *Paederia*, *Hamiltonia*, *Leptodermis*.

The structure of the **cortex** has been very little investigated (see Möller, Vesque, J. E. Weiss, and Douliot). The development of the cork is either superficial or internal. In the first case, either the epidermis (*Sipanea carnea*, *Exostemma floribunda*, *Cephalanthus occidentalis*), or the subepidermal layer of cells (*Pinckneya pubens*, *Rondeletia odorata*, *Burchellia capensis*, *Gardenia florida*, *Cinchona officinalis*, and *C. succirubra*, *Ixora acuminata*, and *I. javanica*), or the next internal cell-layer of the primary cortex (*Rogiera cordata*) becomes the phellogen. As regards the internal formation of cork, the following cases may be distinguished. In *Pavetta indica* it takes place rather far towards the interior of the primary cortex, in *Pagamea guianensis*, Aubl., in its middle portion, in *Coffea arabica*, *Paederia foetida*, *Leptodermis lanceolata*, *Phyllis Nobla*, *Putoria calabrica*, *Bouvardia Jacquini*, and *Serissa foetida* at the external limit of the primary hard bast, in *Galium verum*, L., *G. Schultesii*, Vest, and *Rubia tinctorum*, on the inner side of the suberized endodermis. The tier-like cork ('Etagenkork') of *Pavetta* and *Coffea* is especially remarkable; in these genera consecutive cell-layers of the primary cortex successively develop into a cork-

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[1] Species of the following genera: *Cascarilla*, *Cinchona*, *Portlandia*, *Wendlandia*, *Hedyotis* *Mussaenda*, *Urophyllum*, *Gardenia*, *Retiniphyllum*, *Alberta*, *Ixora*, *Coffea*, *Faramea*, *Lasianthus* *Psychotria*, *Gaertnera*, *Pagamea*, *Chasalia*, *Paederia*.

[2] See Solereder, 1890.

[3] These are: *Hamelia*, *Catesbaea*, *Guettarda*, *Morinda*, *Damnacanthus*, *Coussarea*, *Faramea*, *Psychotria*, *Chasalia*, *Rudgea*, *Paederia*, *Hamiltonia*, *Leptodermis*, *Gaillonia* (here sometimes associated with typical tracheids).

cambium, the activity of which only lasts for a certain time. As to other characters, the cork-cells mostly have thin walls and, at the same time, wide lumina (*Sarcocephalus cordatus*, Miq.), or they are flat and tabular (*Antirrhoea verticillata*, DC., or *Remijia Vellozii*, DC.); thick-walled, usually flattened cork-cells have been observed in *Hymenodictyon excelsum*, Wall., *Buena hexandra*, Pohl, and certain species of *Cinchona*; sclerotic cork-layers, alternating with rows of thin-walled tabular cells, have been found in *Exostemma angustifolium*, R. et Sch. The primary cortex contains typical collenchyma in *Ixora* and *Cinchona*. Diffuse sclerosis is of frequent occurrence in the primary cortex (*Coffea arabica*, L., species of *Buena* and *Cinchona*). The pericycle has a varied structure. According to Möller, isolated groups of hard bast occur in it in *Coffea arabica* and *Ixora acuminata*, Roxb., whereas they are wanting in *Remijia Vellozii*. In the pericycle of the genus *Gaertnera*, I found either (*a*) a continuous or an almost continuous ring of sclerenchyma, consisting of sclerenchymatous elements elongated like rod-cells and shortly articulated, or (*b*) isolated groups of sclerenchyma, consisting of rod-cells. In the secondary bast fibres only occur in rare cases (*Sarcocephalus cordatus*), rod-cells and stone-cells being found in place of them (species of *Antirrhoea*, *Buena*, *Exostemma*, and *Remijia*). The spindle-shaped sclerenchymatous cells which are characteristic of the true China bark, constitute a special form of the rod-cells of the bast; the details of their structure are generally known. In connexion with these rod-cells the crystal-sclerenchyma occurring in the genera *Pavetta* (but not in the closely related genus *Ixora*), *Strumpfia*, and *Webera*, Schreb. (=*Chomelia*, L. + *Stylocoryne*, W. et A.), has still to be discussed. It may be found in the pith, in the primary cortex, and in the bast, and consists of isodiametric or elongated cells, in the walls of which solitary crystals of oxalate of lime are embedded. In *Pavetta Caffra*, Thunb., a study of the development has shown that, as in the hairs of the Guettardeae, the crystals originate in the protoplasm.

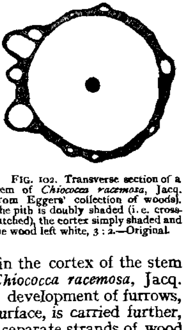

FIG. 102. Transverse section of a stem of *Chiococca racemosa*, Jacq. (from Eggers' collection of woods). The pith is doubly shaded (i.e. cross-hatched), the cortex simply shaded and the wood left white, 3 : 2.—Original.

Anomalous structure of the axis is rare in the Rubiaceae, although the Order contains many lianes. According to Crüger, the lianes which grow in Trinidad and belong to the genera *Chiococca*, *Hillia*, *Uncaria*, and *Amajoua*, possess normal stem-structure. The anomalies occurring in the Order consist in the appearance of furrowed xylem-masses in species of *Lygodysodea*, *Sabicea*, and *Manettia*, which have four longitudinal furrows, according to Crüger (see also H. Schenck with regard to *Manettia luteorubra*, Benth.), and of secondary strands of wood and bast of varying size in the cortex of the stem and in the root (described as *Radix Caincae*) of *Chiococca racemosa*, Jacq. According to Crüger, in the stem of *Sabicea hirta* the development of furrows, as seen in a transverse section and on the external surface, is carried further, inasmuch as a splitting of the entire stem into four separate strands of wood and bast subsequently takes place along the four furrows which were the first to appear; these strands grow in thickness at the periphery and become provided with secondary furrows. The cortical bundles of *Chiococca racemosa* originate in the bast, according to Witte; first a group of vessels is formed, around which a cambium ring appears, producing woody tissue with medullary rays internally and phloem externally.

NOTE.—According to Treub, the tuberous swollen roots of *Myrmecodia*, Gaud., characterized, as is well known, by a labyrinth of chambers and passages, in which ants are always to be found, also possess anomalous structure. This is

connected with the development of the chambers. The primary diarch fibro-vascular system of the root in *Myrmecodia* does not grow in thickness by means of a cambium, as in other Dicotyledonous roots. Instead of this, secondary vascular bundles arise in the parenchyma of the partition-walls; some of this belongs to the primary cortical parenchyma, while the rest consists of phelloderm formed in the course of the development of the chambers; the secondary bundles likewise show no growth in thickness and anastomose freely with one another. The mode of formation of the chambers may be shortly summarized thus: their development commences with the repeated appearance of pocket-like phellogen-layers in the parenchyma of the tuber; these correspond in position to the subsequent cavities, and give rise to cork internally and phelloderm externally; finally, the portions of tissue enclosed by the cork die and give rise to the chambers. (For details see Treub, in Ann. du jard. de Buitenzorg, vol. III, 1883, p. 129 et seq., and Pl. XX–XXIV.)

Literature: Decaisne, Garance, Bruxelles, 1837, 77 pp. and 10 Tab.—Crüger, in Bot. Zeit. 1851, pp. 470 and 490, Tab. vii.—Wigand, in Flora 1856, p. 678 et seq. and Tab. vii.—Karsten, Chinarinden Neu-Granadas, Berlin, 1858.—Vogl, Chinarind. d. Wiener Grosshandels etc., Wien, 1867.—Hanstein, Harz- u. Schleimabs., Bot. Zeit. 1868, p. 712 and Tab. xi.—Vesque, Anat. de l'écorce, Ann. sc. nat., sér. 6, t. ii, 1875.—Delbronck, Pflanzenstach., Hanstein, Bot. Abh., Bd. ii, 1875, pp. 26–7.—Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 45–7 and 341.—De Bary, Vergl. Anat. 1877.—Möller, Rindenanat., 1882, pp. 132–42.—Gardiner, Glands of *Coprosma*, Bot. Centralbl. 1884, ii, p. 31.—Planchon, *Remijia*, Journ. de Pharm. et Chim., sér. 5, t. x, 1884, pp. 329 and 417 et seq.—Volkens, Standort etc., Jahrb. Berliner Gart., Bd. iii, 1884, p. 17 et seq.—Koch, Anat. d. Gatt. *Cinchona*, Diss., Freiburg, 1884.—Michael, Bau des Holzes der Rubiaceen etc., Diss., Leipzig, 1885.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. i, 1885, pp. 192–206 and pl. 9.—Solereder, Holzstr., 1885, pp. 150–4.—Witte, Holz einiger Lianen, Diss., Freiburg u. Kiel, 1886, p. 17 et seq. and Tab.—Radlkofer, Pfl. mit durchs. punkt. Bl., Sitz.-Ber. Münch. Akad. 1886, p. 319.—Eiselen, Rhaphiden, Diss., Halle a. d. S., 1887.—Volkens, Aegypt.-arab. Wüste, 1887, p. 124.—Haeckel, Cystolithes dans le genre *Exostemma*, Bull. Soc. bot. de France 1889, p. 400.—Douliot, Périderme, Ann. sc. nat., sér. 7, t. x, 1889, pp. 382–7.—J. E. Weiss, Korkbild., Denkschr. Regensb. bot. Gesellsch. 1890, separate copy, p. 58.—Volkens, Lack. Blätter, Sitz.-Ber. deutsch. bot. Gesellsch. 1890, p. 133.—Solereder, Gaertnereen, Ber. deutsch. bot. Gesellsch. 1890, General-Versamml., p. 70 et seq., and *Hymenocnemis*, Bot. Centralbl. 1891, ii, pp. 221–2.—Goebel, Pflanzenbiol. Schild. ii, 1891, p. 29 and Tab. xii.—K. Schumann, in Natürl. Pflanzenfam., iv. Teil, Abt. 4, 1891.—Schimper, Indo-malay. Strandflora, Jena, 1891, p. 17.—Solereder, in Natürl. Pflanzenfam., iv. Teil, Abt. 2, 1892, pp. 22 and 26 et seq. and Anat. Charakt. d. Rubiaceen, Bull. de l'Herbier Boissier, vol. i, 1893, pp. 167, 270, and 310 et seq.—H. Schenck, Anat. d. Lianen, 1893, pp. 245–6 and Tab. xii.—Russell, Climat. méd., Ann. sc. nat., sér. 8, t. i, 1895, p. 348.—Grevillius, in Engler, Bot. Jahrb., Bd. xxiii, 1896, p. 70.—Wittlin, Oxalattasch., Bot. Centralbl. 1896, iii.—Warming, Halofyt Stud., K. Danske Vid. Selsk. Skr. 1897, pp. 187, 195, 203 and 234.

VALERIANEAE.

Our knowledge of the anatomy of this small Order, consisting of herbaceous plants only, embraces the following facts. The **leaves** have bifacial structure, in so far as they have been investigated (*Valeriana officinalis* and *V. Phu*, *Centranthus ruber*, *Valerianella coronata*). The stomata possess no special subsidiary cells; their development follows the type found in the Cruciferae. They occur either on both surfaces of the leaf, or, as in *Valeriana officinalis*, on the lower surface only. Water stomata are recorded on the leaf-teeth of *Valeriana sambucifolia*. The hairy covering consists of simple and glandular hairs. The former have thick walls and are generally unicellular, and are either short (*Valerianella olitoria*) or long and pointed (*Valeriana officinalis*); occasionally these simple hairs become multicellular, owing to the formation of delicate transverse walls (*Valeriana sambucifolia*). According to Vesque and Grignon, the small glandular hairs have a uni- or multicellular stalk and a small multicellular head. Crystalline elements have not been observed. The deposition of a secretion in the roots of the Valerianeae, which is mentioned by Meyen (according to De Bary) and by Chatin and Grignon especially in *Nardostachys* and species of *Valeriana*, requires further examination. According to Zacharias, somewhat elongated cells, containing ethereal oil and having suberized walls, occur in the subepidermal layer of the root of *Valeriana*

officinalis. As regards the structure of the **axis** it may in the first place be mentioned that, according to the statements found in the literature, the outermost cell-layers of the primary cortex are collenchymatous, that there is a distinct, large-celled endodermis, whereas hard bast is wanting, and that the vascular bundles are separated from one another by more or less strongly developed medullary rays. The branch of *Centranthus ruber*, DC., which I examined, showed a closed ring of xylem with (*a*) wood-prosenchyma bearing simple pits, (*b*) vessels possessing scalariform perforations in the neighbourhood of the primary wood but elsewhere simple perforations, and (*c*) no distinct ray-parenchyma. In the root the development of the cork is superficial in *Valeriana officinalis* and *V. Phu*, pericyclic in *Valerianella coronata* and *Centranthus ruber*.

Literature: [Chatin, Ét. sur les Valérianées etc., Thèse, Paris, 1871, and Mém. Soc. biol., iv, 1872, p. 3].—De Bary, Vergl. Anat. 1877.—Zacharias, in Bot. Zeit. 1879, p. 635.—Grignon, Caract. anat. des Lonicérinées etc., Thèse, Paris, 1884.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. 1, 1885, pp. 206–7.—Parmentier, in Ann. sc. nat., sér. 8, t. ii, p. 18 et seq.

DIPSACEAE.

Our information regarding the most important anatomical features in this Order is chiefly derived from Vesque and Grignon.

The structure of the **leaf** may be bifacial (*Scabiosa columbaria*, &c.) or centric (*Scabiosa caucasica, Dipsacus azureus*). Stomata usually occur on both surfaces of the leaf and are generally surrounded by several ordinary epidermal cells, more rarely by three only; in the latter case the arrangement agrees with the Cruciferous type, one cell being smaller than the other two. Hypoderm is mentioned by Pfitzer as occurring in *Dipsacus sylvestris*. The vascular bundles of the veins have no sclerenchyma; they are either embedded or vertically transcurrent by means of thin-walled tissue (*Dipsacus*). The hairy covering consists of clothing and glandular hairs. The former are unicellular and are occasionally (species of *Dipsacus, Knautia*, and *Succisa*) seated upon a multicellular emergence of varied length. The glandular hairs may either have a short stalk and a head composed of few cells (*Dipsacus*[1], *Cephalaria, Scabiosa*) or a long uniseriate stalk with a head consisting of a larger number of cells (*Knautia*). In connexion with the trichomes we may mention the spiny structures found in *Dipsacus*, in the formation of which both epidermis and periblem take part, as well as the glandular leaf-teeth of *Knautia ciliata* and *Cephalaria procera*, which, according to Reinke, contain the termination of a vein, provided with epithema, and surmounted by a few stomata. Oxalate of lime has been met with in the leaf and axis of certain species in the form of clustered crystals. Of secretory elements, sacs, which have wide lumina and are considerably elongated in the vertical direction, are the only form known; they occur in the pericycle of the axis (Grignon and Van Tieghem) in *Dipsacus fullonum, D. sylvestris, D. Gmelini*, and other species.

With regard to the structure of the **axis** in *Dipsacus laciniatus*, L., and *Succisa pratensis*, Moench, the following facts, based on my own observations, may be mentioned. The transverse section shows a closed ring of wood and bast, traversed by uniseriate or biseriate medullary rays and separated from the primary cortex by a suberized endodermis. Bast-fibres are absent. The xylem-mass

[1] The glandular hairs, which occur on the inner surface of the water-receptacles, formed by the leaf-sheaths in *Dipsacus sylvestris* and other species of *Dipsacus*, bear curious small bodies of rounded shape on their surface; these give rise to numerous long threads, which perform various movements with great energy, when placed in a suitable medium. According to Cohn and Chodat, the small bodies and threads in question are secretory formations, but this is contrary to the view of Darwin, who attributed a protoplasmic nature to them (see Chodat, Arch. sc. phys. et. nat. de Genève, 1892, pp. 89 and 116 and Plate, as well as the earlier literature cited there).

in addition to the medullary rays, with cells more or less strongly elongated in an axial direction, contains the following elements : (*a*) vessels, the perforations of which are scalariform only in the neighbourhood of the primary wood (except in *Succisa* where such perforations occur to some extent also in the secondary wood), elsewhere they are simple and of elliptical outline; and (*b*) wood-prosenchyma, which has rather thick walls and bears simple pits in *Dipsacus*, whilst it is, for the most part, provided with distinct bordered pits in *Succisa*. According to Vesque and Douliot, the cork is developed subepidermally in *Knautia sylvatica*, in the pericycle in *Dipsacus* and *Cephalaria*. Lastly, we may mention the girdle-like connecting strands, which Hanstein demonstrated in the nodes of *Dipsacus*, *Knautia*, *Scabiosa*, and *Succisa*.

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CALYCEREAE.

At the present time there are scarcely any statements to be found in the literature with regard to the anatomy of this small Order, which is very closely related to the Compositae. On the basis of investigations on *Acicarpha spathulata*, R. Br.[1], and *Boopis spathulata*, Philippi, it may first be pointed out that both internal secretory receptacles and external glands are absent, and that the stomata, which occur on both surfaces of the leaf in the two species named, have no special subsidiary cells, but are surrounded by an indefinite number of neighbouring cells. A transverse section of the branch of *Acicarpha* shows a circle of vascular bundles, surrounding a pith, which consists of unlignified parenchyma containing abundant clustered crystals; the bundles are separated from one another by rather broad medullary rays, lignified in the internal, unlignified in the external portion. The wood contains: (*a*) vessels with rather wide and rounded lumina, simple perforations and bordered pitting on those parts of their walls which are in contact with parenchyma of the medullary rays; (*b*) wood-prosenchyma which has rather wide lumina and fairly thick walls, and bears simple pits: secondary medullary rays are wanting. To the exterior of the phloem-groups strands of sclerenchymatous elements resembling rod-cells are present, intermingled with cells resembling bast-fibres. The primary cortex is rich in clustered crystals.

COMPOSITAE.

1. Review of the Anatomical Features. The following features are characteristic of this Order: the superficial development of the cork; the simple perforations of the vessels, side by side with which scalariform perforations may occasionally appear in smaller numbers; the simple pitting of the wood-prosenchyma, which is occasionally septate; the absence of oxalate of lime or its excretion in the form of small needles, small octahedra, and small prisms (rarely in the form of the ordinary large rhombohedra or of clustered crystals); and the occur-

[1] Cf. Warming, Halofyt-Studier, K. Danske Vid. Selsk. Skr. 1897, pp. 196–7. In alcohol-material of the leaf sphaero-crystals have been observed.

rence of inulin. The stomata are surrounded by three or more epidermal cells. The varied differentiation of the internal secretory organs is important for the subdivision of the Order. Schizogenous resin-canals, which originate in the root, leaf, and stem by the division of endodermal cells, are found (at any rate in the root) to be widely distributed in the Tubuliflorae, and also occur frequently in the Labiatiflorae and in a few Cichoriaceae (root of *Scorzonera* and *Scolymus*). In addition to the endodermal resin-canals, others, situated in the pith or in the primary cortex, appear in certain species belonging to these groups; additional resin-canals arise in the secondary bast of stem and root, and occasionally also in the wood of the root in species possessing secondary growth. Secretory cavities have been met with in the leaves of the genera *Bigelovia, Pectis, Porophyllum,* and *Tagetes*; elongated secretory cells occur in the genera *Carduus, Carlina, Cirsium, Lappa, Silybum,* and *Vernonia*. Just as the resin-canals are distinctive of the Tubuliflorae, the laticiferous vessels are characteristic of the Cichoriaceae. Primarily these laticiferous elements form two separate systems, of which one is situated in the primary bast of the root, being developed on the inner side of the groups of sieve-tubes, whilst the other belongs to the pericycle of the stem. Amongst the Tubuliflorae laticiferous tubes are known in the genus *Gundelia* only. The hairy covering consists of clothing and glandular hairs. The clothing hairs are generally uniseriate and occasionally form the starting-points from which a silicification of groups of epidermal cells proceeds; they are more rarely biseriate or multiseriate (shaggy hairs, frequent in the Cichoriaceae). The following are special forms of the uniseriate clothing hairs: those in which the long terminal cells are narrow and developed in the form of a whip (in numerous genera, see special part); two-armed hairs (species of *Anthemis, Artemisia, Chrysanthemum* incl. *Balsamita, Olearia, Pyrethrum, Santolina*); stellate or small scale-like trichomes with a unicellular terminal portion, developed in a radiate or scale-like form (*Eremanthus, Hieracium, Olearia, Piptocarpha*). A specially remarkable variety of shaggy hair, possessing a two-armed terminal cell, has been observed in *Picris*. The glandular hairs, which are widely distributed in the Order, are polymorphic. Bladder-like external glands, with a short stalk and an ellipsoidal biseriate head, are most abundant. The following special or anomalous structural features of the axis occur: the appearance of a furrowed xylem-mass, similar to that of the Bignonieae (undetermined stem of H. Schenck's No. 366, *Mikania, Bidens*); *Aristolochia*-structure (in *Mikania* and *Bidens*); the formation of secondary bundles of wood and bast (species of *Coreopsis, Mikania* and *Kleinia*, also *Dahlia imperialis*); the occurrence of medullary groups of soft bast or of medullary vascular bundles (in numerous Cichoriaceae, and in species of *Gundelia, Helenium,* and *Obeliscaria*), and of cortical vascular bundles (species of *Ammobium, Centaurea, Gundelia, Helenium,* and *Senecio*).

2. Special Anatomical Diagnosis. Owing to the great extent of the Order our knowledge of the anatomical features is still imperfect. The following subjects will be considered in the order given: the hairy covering, the internal secretory receptacles (oil-canals, oil-cavities, laticiferous vessels, and secretory cells), the mode of excretion of oxalate of lime, the little that is known about the structure of the leaf, and lastly the structure of the axis.

The **hairy covering** is rather varied, and consists of clothing and glandular hairs. The clothing hairs are either uniseriate or composed of two or more rows of cells (shaggy hairs in the second case). Unicellular clothing hairs are not recorded in any member of the Order[1]. The uniseriate trichomes in the simplest case consist of cells that are all similar to one another, except that the terminal cells are pointed or rounded off (*Taraxacum officinale, Chondrilla*

[1] With the exception of the laticiferous hairs of the Cichoriaceae, which will be considered in connexion with the laticiferous tubes.

juncea, &c.). Special forms arise from the basal cells (stalk-cells) being short, whilst the terminal cells are elongated. To this type of trichome belong, firstly, those forms in which the basal and terminal cells are of the same breadth, and the terminal cells lie in the same direction as the stalk-cells, e.g. trichomes with several terminal cells, placed in a row, found by Vuillemin in species of *Bellis*, *Inula*, and *Doronicum*; and further trichomes, each with a single terminal cell, observed by Vesque in species of *Palafoxia*, *Catananche*, and *Vernonia*, and by Vuillemin in *Matricaria*. In these

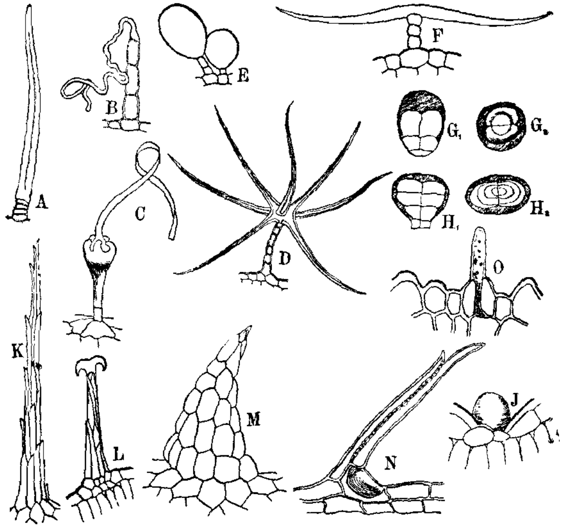

FIG. 103. Hairy covering of the Compositae: A, *Catananche coerulea*, L. B, *Cirsium lanceolatum*, Scop. C, *Carlina vulgaris*, L. D, *Olearia stellulata*, DC. E, *Zollikoferia nudicaulis*, Boiss. F, *Artemisia Absinthium*, L. G, *Mikania pubescens*, Nutt. H, *Chrysanthemum cinerariaefolium*, Vis. J, *Achillea fragrantissima*, Schultz Bip. K, *Hypochaeris aetnensis*, Benth. et Hook. L, *Picris coronopifolia*, DC. M. *Urospermum picroides*, F. W. Schmidt. N, *Spilanthes oleracea*, L. (floral region). O, *Lactuca Scariola*, L.—A, B and K after Vesque; E, J and L after Volkens; G, H and N after Vogel; C, D, F and M Original.

latter we meet with minor modifications which concern the structure of the cell-walls; thus in *Catananche* (Fig. 103, *A*), for instance, the four basal cells have thin walls, whilst the terminal cell is thick-walled and has a narrow lumen; again in species of *Vernonia* the terminal cell has thin walls and the stalk-cells thick walls (Vesque), and so on. According to Volkens, the trichomes of *Brocchia cinerea*, Vis. differ from those just discussed in the possession of a long, thin-walled terminal cell, which is placed at an angle to the stalk, and a few short basal cells. In the trichomes already mentioned with an elongated terminal cell, the stalk and terminal cell are of uniform breadth; in another type of hair, which is very widely distributed, the

terminal cell is much narrower, usually very long and frequently curled like a lash; it is seated on a broad uniseriate pedestal, which is like the handle of the whip. The cobweb-like hairy covering of the leaves of many Compositae consists of trichomes of this kind. They are mentioned by Vesque as occurring in species of *Anandria, Antennaria, Cineraria, Cirsium* (Fig. 103, *B*), *Petasites*, and *Serratula*, by Volkens in species of *Atractylis, Artemisia, Echinops, Ifloga, Phagnalon*, and *Pulicaria*, by Vuillemin in species of *Achillea, Anthemis, Carlina, Gnaphalium, Helichrysum, Silybum*, and *Tripolium*, by Grignon in *Centaurea, Cynara*, and *Lappa*. The terminal cell of these hairs when mature is always dead. Differences occur in these trichomes with regard to the structure both of their basal portion and of the terminal cell. In this connexion it may be mentioned that the lumen of the terminal cell may become confined to the lowest portion of the hair, the remainder being almost completely solid (Volkens) (e.g. in *Echinops spinosus*, L., or *Pulicaria undulata*, DC.), while in other cases (e.g. in *Petasites*) the terminal cell has thin walls and is filled with air; further, in *Carlina vulgaris*, L. (Fig. 103, *C*) the upper cell of the bicellular stalk is broadened out above in the shape of a club and produced apically into 4–8 papillae, which are bent inwards and embrace the base of the terminal cell. The above-mentioned trichomes of *Brocchia cinerea* form a transition to the two-armed hairs which have been observed by Hildebrandt, Vesque, Volkens, and Vuillemin in species of *Anthemis, Artemisia* (Fig. 103, *F*), *Chrysanthemum* (incl. *Balsamita* and *Pyrethrum*), and *Tanacetum*, and by myself in *Santolina Chamaecyparissus*, L. (contrary to Vuillemin's statement regarding this species), *Olearia argophylla*, F. v. Muell. and *O. viscosa*, Benth. The stalk of these Malpighian hairs consists of a row of cells, whereas the terminal portion, which has equal or unequal arms, is unicellular. Closely related to the two-armed hairs are the stellate hairs and the small scale-like structures of the Compositae; this relation is indicated by the fact that one finds the two types of hairs within the same genus (*Olearia*), according to my observations, as well as by the signs of transitional forms between the two-armed hairs and the stellate type in *Santolina Chamaecyparissus*, as shown by the occurrence of local protrusions on the arms of its hairs. In correspondence with this relation the stellate and peltate hairs of the Compositae consist of a uniseriate stalk and of a terminal cell, which is stellately branched or developed as a small scale. To this type belong the stellate hairs of the species of *Hieracium* with a thin-walled terminal cell, those of *Olearia stellulata*, DC. (Fig. 103, *D*), with a thick-walled ray-portion, and the small, scale-like structures of *Eremanthus incanus*, Less., *Piptocarpha macropoda*, Bak. and *P. Lechleri*, Bak. The candelabra-hairs of *Andryala sinuata*, described by Vuillemin, may be interpreted as a modification of the stellate hairs in question; here the upper portion of the trichome consists of several stellately-branched cells, placed one above the other. According to Rauter, reduced candelabra-hairs, i.e. such as possess only two stellately-differentiated cells besides the stalk, occur in *Hieracium* (*H. aurantiacum*, L., and *H. Pilosella*, L.). Finally, we may mention the bladder-like trichomes of *Reichardia tingitana*, Roth, and *Zollikoferia nudicaulis*, Boiss. (Fig. 103, *E*), observed by Volkens, in which a uniseriate stalk of varied length is crowned by a spherical cell; these hairs are not glandular, but are probably rich in cell-sap. The shaggy or multiseriate hairs are specially widely distributed in the Cichoriaceae; more rarely they occur elsewhere, as in *Cirsium*, according to Wunderlich. They form slender, broadly conical or wart-like structures and consist of a varied number of cell-rows. Special forms of these shaggy hairs are: (*a*) the slender trichomes of the species of *Hieracium* or of *Hypochaeris aetnensis*, Benth. et Hook. (Fig. 103, *K*), in which the epidermal cells of the hair are somewhat elongated and project in a papillose manner at their upper ends; (*b*) the shaggy hairs of *Picris coronopifolia*, DC. (Fig. 103, *L*), which have a two-armed, anchor-

shaped terminal cell; (*c*) the well-known forked shaggy hairs of *Leontodon hastilis*, L., the 2–3 uppermost cells of which are radially produced; and (*d*) the broadly conical shaggy hairs of *Urospermum picroides*, Schmidt (Fig. 103, *M*), which are crowned by a small pointed cell. In the floral parts the shaggy hairs undergo a peculiar reduction, inasmuch as they often consist of two cells only, united by their longitudinal walls (Fig. 103, *N*).

External glands are widely distributed. They are frequently depressed below the leaf-surface, and then occasionally give rise to pellucid dots (*Ageratum conyzoides*, L., *Baccharis Douglasii*, DC., *Mikania scandens*, Willd.). Structurally they are either glandular hairs with a uniseriate stalk of varied length, or glandular shaggy hairs with a multiseriate stalk; in some cases they are probably of the nature of glandular emergences. The head varies in shape and is variously constituted, being generally irregularly subdivided by horizontal as well as vertical walls. According to Martinet, the glandular shaggy hairs occur, for example, in species of *Andryala*, *Calendula*, *Madia*, *Hieracium*, *Sonchus*, *Siegesbeckia*, and *Tripteris*; the structure of the head in *Andryala sinuata* must be specially mentioned, since its epidermal cells are produced in the form of papillae. Short-stalked glandular hairs (Fig. 103, *G*, *H*), the head of which consists of two rows of cells, form a special type of external glands, occurring in very many cases (species of *Anthemis*, *Artemisia*, *Asteriscus*, *Baccharis*, *Balsamita*, *Brachylaena*, *Cephalophora*, *Cosmophyllum*, *Conoclinium*, *Chrysanthemum*, *Francoeuria*, *Gnaphalium*, *Helianthus*, *Inula*, *Kleinia*, *Lappa*, *Mikania*, *Olearia*, *Pulicaria*, *Pyrethrum*, *Symphyopappus*, *Tanacetum*, and *Xanthium*). It is an interesting fact that, according to Vuillemin, these biseriate glands are orientated on the stem in such a way that the dividing wall between the two rows of cells is either regularly placed in the transverse plane of the stem (species of *Anthemis*, *Artemisia*, *Balsamita*, *Lappa*, and *Pyrethrum*), or in the radial plane (*Inula*, *Xanthium*). In addition to the glands with biseriate heads, Vuillemin also observed uniseriate (in species of *Cynara* and *Echinops*) and quadriseriate heads (*Doronicum*). The secretory organs, observed by Volkens in species of *Artemisia*, *Achillea*, *Brocchia*, and *Centaurea*, may be added to the list of external glands just discussed; the organs in question consist of one or more cells, which are slightly depressed below the level of the neighbouring epidermal cells and have thinner external walls; the secretion collects below the cuticle, *which is swollen like a bladder. The peculiar laticiferous hairs of the* Cichoriaceae will be mentioned in connexion with the description of the laticiferous vessels.

Occasionally the glandular hairs extrude so much secretion on the surface of the leaf, that the latter has a varnished appearance. Such varnished leaves are recorded by Volkens in species of *Baccharis*, *Brachylaena*, *Eupatorium*, *Gochnatia*, *Helianthus*, *Haplopappus*, *Olearia*, and *Symphyopappus*. The external glands, to the agency of which this phenomenon is due, are in many cases the bladder-like biseriate glands, a number of which are arranged together in groups, intermingled with peculiar uniseriate whip-like hairs. The varnished leaves of *Vernonia viscidula*, Less. and *Celmisia vernicosa*, Hook. f. do not owe their appearance to external glands. In the former plant subepidermal idioblasts, filled with resin, are perhaps the cause of the coating of varnish; the latter possesses a cuticle, which exfoliates readily and is covered with a thin stratum of varnish.

At this point we may notice the glandular excretions, occurring, according to Reinke, on the leaf-teeth of *Mulgedium macrophyllum*, *Tussilago fragrans*, *Aster Novae Angliae*, &c.; these excretory organs contain mucilage-bearing cells and usually also the termination of a vein, whilst they are crowned by a group of water-pores.

Schizogenous **resin-canals** are found only in a certain number of the Compositae; they are very widely distributed in the Tubuliflorae, are not so common in the Labiatiflorae, and only occur in a few Cichoriaceae. Generally they traverse the stem, leaf, and root. In all these organs of the plant they are

chiefly of endodermal origin, as Sachs first observed, and as has been subsequently pointed out, especially by Van Tieghem and Vuillemin. In those species which possess resin-canals, some of them invariably originate through the division of cells of the endodermis. The endodermal resin-canals are thus characteristic of the Order. Those of the root have no special epithelial cells, but are directly surrounded by the cells of the double endodermis; they are arranged in arcs opposite the groups of bast belonging to the primary fibro-vascular system. In the leaf and branch the endodermal resin-canals are generally provided with an epithelium and mostly lie adjacent to the endodermis on its external side either opposite the vascular bundles or in an interfascicular position.

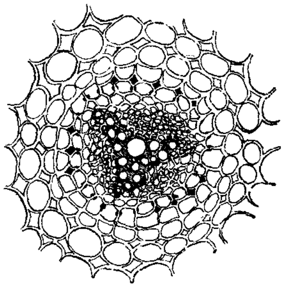

FIG. 104. Transverse section through the internal portion of the young root of *Inula Helenium*, showing the early stages of development of the oil-canals in the endodermis, which is undergoing division.—After Triebel.

Concerning the development of the epithelium, see Vuillemin. When the secretory canals have a very wide lumen, some of the epithelial cells occasionally project into the secretory space, and thus look like internal glands (old rhizomes of *Arnica montana* and *Centaurea Scabiosa*). Van Tieghem and Vuillemin met with resin-canals devoid of epithelium in the stems or rhizomes of certain species of *Adenostyles, Aronicum, Biotia, Cacalia, Cineraria, Cirsium, Doronicum, Eupatorium, Homogyne, Nardosmia, Palafoxia, Petasites, Senecio, Serratula, Stevia*, and *Tussilago*. They are, however, probably of little value as an anatomical character, since resin-canals devoid of epithelium and others provided with it occasionally occur side by side in the same plant (*Lasthenia glabrata, Cynara corsica*); again, the canals without an epithelium do not always appear in all the species of a genus (*Cacalia, Senecio*). Resin-canals, situated internally to the endodermis, are very rare in the stem (*Senecio cordatus* and *S. Cineraria*).

The endodermal resin-canals of the root and stem exhibit further differences as regards their diameter and the number of canals occurring opposite the primary bast-groups (of the root) or the vascular bundles or interfascicular tissue, as the case may be (see the examples given by Van Tieghem, 1872, p. 125, and p. 130 et seq.). According to existing investigations, the most useful feature for systematic purposes (mostly as a generic character) is the position of the resin-canals in the stem, whether opposite the vascular bundles or between them, although displacements may occasionally arise owing to the phenomena of secondary growth. According to Van Tieghem, Hildebrandt, and Vuillemin, endodermal resin-canals, opposite the vascular bundles, are found in the stems of the following genera: *Adenostyles, Aronicum, Aster, Bellis, Biotia, Cacalia, Carlina, Carthamus, Cenia, Centaurea, Cineraria, Cnicus, Cynara, Doronicum, Dracopis, Flaveria* pro parte, *Microlonchus, Petasites, Senecio, Serratula, Xanthium*; on the other hand, resin-canals which are interfascicular in position are found in *Achillea, Achyropappus, Actinomeris, Anacyclus, Anthemis, Arnica, Artemisia, Balsamita, Calliopsis, Chrysanthemum, Cirsium, Cladanthus, Dahlia, Echinacea, Eupatorium, Flaveria* pro parte, *Galinsoga, Helianthus, Heliopsis, Hymenoxys, Inula, Lasthenia, Lonas, Madia, Matricaria, Ormenis, Parthenium, Ptarmica, Pulicaria, Pyrethrum, Santolina, Sanvitalia, Silphium, Silybum, Tagetes, Tanacetum, Zinnia*.

In addition to the endodermal resin-canals, which form the type characteristic of the Order, others situated in the pith or primary cortex and in the secondary tissues of the vascular system also occur in the stem in certain cases. Resin-canals, situated in the primary cortex of the stem, and present in an analogous position in the veins of the leaf, are mentioned by

Van Tieghem as occurring in species of *Solidago* (incl. *Kleinia*) only, e. g. *S. Kleinia*. On the other hand, those situated at the periphery of the pith are commoner; Van Tieghem observed them either singly or several together opposite each vascular bundle in species of *Ageratum, Carduus, Dahlia, Helianthus, Serratula, Solidago*, and *Spilanthes*; Hildebrandt found them in species of *Actinomeris, Artemisia, Bidens, Calliopsis, Coreopsis, Cosmos, Doronicum, Echinacea, Galinsoga, Guizotia, Helianthus, Heliopsis, Iva, Lindheimera, Obeliscaria, Parthenium, Silphium, Sogalgina* (canals here scattered in the pith), *Spilanthes, Xanthium*, and *Ximenesia*. The secretory canals of the secondary tissues may occur in the wood and bast; in the former, however, they probably only occur in subterranean organs, as appears from the investigations hitherto carried out. Thus, according to Van Tieghem, they are found in the secondary wood and bast of the root of *Inula Helenium* [1], in the root of *Carlina acaulis* and of the *Anacyclus Pyrethrum* of commerce; likewise in the secondary bast of the branch and root of *Centaurea atropurpurea* and *Helianthus tuberosus*. It may be added that in *Echinops exaltatus* and *Tagetes patula* the resin-canals of the bast are replaced by resin-cells in the medullary rays of this tissue.

The pericycle and the primary portions of the vascular system are, as a rule, without resin-canals. According to Van Tieghem and Vuillemin, *Ambrosia trifida* alone forms an exception; here resin-canals occur internally to the primary arcs of hard bast at the limit of pericycle and soft bast, and in some cases also at a greater depth in the tissue of the latter.

In the Tubuliflorae, if resin-canals are present at all, they always occur in the root, the hypocotyledonary stem of the seedling and the cotyledons. But above the level of the cotyledons (i.e. in the foliage-leaf and stem) they may occasionally be wanting; according to Van Tieghem, Vuillemin, and Hildebrandt, this is the case in species of *Ammobium, Anthemis, Baeria, Calendula, Carduus, Centaurea, Cirsium, Echinops, Eupatorium, Filago, Galactites, Gnaphalium, Helenium, Helichrysum, Inula, Leyssera, Madaria, Pinardia, Podolepis, Rhynchopsidium, Scolymus, Sphenogyne, Tripteris*, and *Vernonia*. But even in those cases in which the axis contains well-developed resin-canals, they may sometimes be wanting in the lamina of the leaf, in consequence of their only penetrating as far as the leaf-base (*Xeranthemum cylindraceum, Cirsium arvense*, &c., according to Van Tieghem).

Finally, details may be given of the distribution of oil-canals in the Order. As has been repeatedly mentioned the majority of the Tubuliflorae possess these secretory organs, at any rate in their roots. They are also common in the Labiatiflorae, investigated by Van Tieghem. The secretory canals are here without exception of endodermal origin. Resin-canals, situated in the pith or in the primary cortex, have not been observed in any member of the Labiatiflorae.

Concerning the distribution of the resin-canals in the Labiatiflorae Van Tieghem makes the following statements. In the root they have been observed in *Stifftia chrysantha, Gerbera Schimperi, Leria integrifolia, Calopappus acerosus*, &c., whilst in *Chaptalia tomentosa* only an oil-containing endodermis has been met with, and in *Barnadesia* even this is wanting. In the branch and leaf the resin-canals have been demonstrated in *Ainsliaea acerifolia, Hyalis spartioides, Lycoseris mexicana, Mutisia retusa, Nassauvia digitata*, and *Polyachyrus villosus*; they occur, from one to three in number, mostly external to the arcs of hard bast of the pericycle, but between them in *Nassauvia*. The following genera have no resin-canals in the branch or leaf: *Barnadesia, Calopappus, Chaetanthera, Chaptalia, Chuquiragua, Dicoma, Flotovia, Fulcaldea, Gerbera, Gochnatia, Leria, Lucilia, Moquinia, Onoseris, Proustia, Schlechtendalia, Stifftia*, and *Triptilion*.

Amongst the Cichoriaceae an interesting case occurs in *Scorzonera* and *Scolymus grandiflorus*, according to Van Tieghem, for the root, besides possessing

[1] The intercellular secretory receptacles, occurring in the secondary wood and bast of *Radix Helenii*, are not canals according to Triebel, but elongated oil-cavities, closed on all sides.

laticiferous vessels, contains resin-canals, which are situated in the double endodermis external to the primary bundles of bast. *Tragopogon porrifolius* shows a similar feature, according to the same author, but in this case the canals contain no oil. A similar doubling of the endodermal layer has also been met with in *Cichorium Intybus* and *Lampsana communis*, but the oil-canals are wanting. Finally, in some other Cichoriaceae, such as *Hieracium*, *Hypochaeris*, *Lactuca*, &c., even the double endodermis is absent.

Secretory cavities have only been observed in a few members of the Order, namely, in the genera *Tagetes*, *Porophyllum*, *Bigelovia*, and *Pectis*, according to Van Tieghem, Bokorny, Radlkofer, and Warming. In these genera they give rise to transparent dots or fine striae in the leaf. Their origin is stated to be schizogenous in *Tagetes*, lysigenous in *Porophyllum*; in *Porophyllum ruderale*, Cass. the secretory cavities are enveloped by fine branches of the vascular system.

In the same way as the endodermal resin-canals are distinctive of the Tubuliflorae and Labiatiflorae, **laticiferous vessels** are characteristic of the Cichoriaceae; these latter are found in the root as well as in the stem and leaf. The laticiferous tubes of the stem and leaf form a special system of their own, which is distinct from the laticiferous system of the root. The former system belongs to the outermost cell-layer of the pericycle, which borders directly on the endodermis. Additional laticiferous tubes arise in the secondary bast of the stem, and in those Cichoriaceae which are characterized by the presence of medullary phloem-bundles in the stem, there are further laticiferous tubes situated at the periphery of the latter. In the leaf the laticiferous tubes generally follow the course of the vascular bundles of the veins; in *Hypochaeris radicata* they are described as penetrating into the mesophyll (Haberlandt, Groom and Scott). The primary laticiferous vessels occupy quite a different position in the root. Here they occur at the internal margin of the primary phloem. Subsequently secondary laticiferous tubes are also developed in the secondary bast of the root. The primary laticiferous system of the root is however connected with the primary system of the stem, for at a certain level both systems are found to be present in a transverse section and are united with one another by anastomoses. With regard to the contents of the laticiferous tubes it may be mentioned that a protoplasmic body and nuclei have been shown by E. Schmidt to be present; the size of their lumen varies, and may be very small (e.g. in *Urospermum Dalechampii*), of medium size (in *Cichorium Intybus*), or very wide (in *Chondrilla juncea*, *Lampsana communis*, &c.).

In connexion with the laticiferous tubes of the Cichoriaceae the laticiferous hairs (Fig. 103, *O*) may be shortly referred to; they have been observed on involucral and other bracts in the genera *Lactuca*, *Mulgedium*, *Prenanthes*, *Sonchus*, and *Picris*, and cause the excretion of latex that is observed when the involucral leaves of the plants mentioned are touched (Carradori, Trécul, Delpino, Piccioli, Kny, and Zander). The laticiferous structures in question, which were first regarded by Delpino as an arrangement for keeping injurious insects away from the flowers, are single epidermal cells developed as hairs; together with two or more neighbouring cells, likewise belonging to the epidermis, they become united with the free terminal branches of the laticiferous system accompanying the vascular bundles, by the absorption of portions of the intervening walls; the hairs themselves thus represent terminations of the laticiferous system. Regarding their varied mode of differentiation see Zander, loc. cit.

Outside the Cichoriaceae, laticiferous vessels have only been met with in one member of the Tubuliflorae, viz. in *Gundelia Tournefortii*, L. The stem of this plant contains laticiferous tubes in the pericycle and in the neighbourhood of the bast of the medullary vascular bundles; the leaf possesses these elements in the veins and they also occur free in the mesophyll. It may be added that resin-canals are wanting in the leaf and stem of *Gundelia*.

Finally, isolated elongated **secretory cells** with resinous or milky contents occur in some cases. They occupy the same position as the laticiferous tubes, that is to say, in the stem and leaf they are present in the pericycle within the endodermis and external to the primary hard bast (to which secretory cells, developed in the secondary bast, are added) and in the root in the innermost portion of the primary phloem. In *Carduus*, *Cirsium*, *Lappa*, and *Silybum*, they are confined to stem and leaf, whereas in *Vernonia* they have been found in the root as well.

Oxalate of lime is excreted in the form of acicular, prismatic, or small octahedral crystals. True raphides are wanting, but occasionally the bundles of acicular crystals come to resemble bundles of raphides (mesophyll of *Carlina vulgaris*). Large solitary crystals (cortex of *Kleinia articulata*, Haw., and *Cacalia repens*; pith of *Othonna arborescens*, L.) and clustered crystals (pith of *Kleinia repens*, Haw.) are rare (Joh. Müller and Vuillemin). **Inulin**, which is so characteristic of this Order, occurs especially in the tissues of the root, but occasionally also in the leaf (Joh. Müller) and stem; in the latter it accompanies starch (Ahlfoengren). Other sphaero-crystals, occurring in certain members of the Order, consist of gypsum, according to Kohl.

The **structure of the leaf** has so far been comparatively little investigated. The stomata are surrounded by three or more ordinary epidermal cells, according to Vesque; in their development they follow the Cruciferous type; this, however, is obscured in the fully-developed leaf. The epharmonic features of the leaf-structure vary; under this heading are included: (*a*) the distribution of the stomata on the leaf-surfaces, (*b*) the position of the guard-cells with regard to the level of the epidermis (seated on a cylindrical tube in *Cineraria cruenta* and in *Haplopappus* and *Gochnatia*), (*c*) the development of hypoderm on the upper side of the leaf (*Senecio Munroi*, Hook. f., *Celmisia vernicosa*, Hook. f., and *C. Lyallii*, Hook. f.), (*d*) the differentiation of the mesophyll and fibro-vascular system (including the development of a sheath of cells with wide lumina around the vascular bundles of the veins, and the radiate arrangement of the cells of the palisade tissue around this sheath in *Pectis humifusa*, Sw.), (*e*) the excretion of wax on the surface of the leaf (species of *Hieracium* and *Kleinia*). In this connexion the characteristic leaf-structure of a few biologically interesting forms may be briefly pointed out; such structures occur in: (*a*) the rolled leaves of *Olearia Solandri*, Hook. f. (Diels); (*b*) the scale-like leaves of *Lepidophyllum quadrangulare*, *Phaenocoma prolifera*, *Ozothamnus Selago*, *O. microphyllum*, and *O. coralloides*, in which the lower side of the leaf becomes external and is sometimes (*Ozothamnus*) distinguished by an exceptionally thick outer wall and cuticle, while it is usually only the upper surface of the leaf that bears stomata (Goebel, Lazniewski, Diels); (*c*) finally, the leaves of *Celmisia Lyallii*, Hook. f., which in appearance and structure remind one of a steppe-grass, and in which the sclerotic hypoderm, developed in great quantity beneath the upper surface of the leaf, traverses the mesophyll in the form of plates, enclosing the vascular bundles of the veins and also forming a massive lower hypoderm in the projecting portions of the lower surface of the leaf. Of special anatomical features in the leaf-structure the not uncommon occurrence of silicified groups of cells in the epidermis remains to be mentioned. Here, as in other cases, the hairs are usually the centres from which silicification starts. Silicified rosettes of cells, bearing a hair or a rudiment of a hair, are found, for example, in *Helianthus*, *Obeliscaria*, and *Heliopsis* (Mohl, De Bary); in *Helianthus giganteus*, L., some of the cells of these rosettes contain cystolith-like structures, which are encrusted with carbonate of lime in the same way as the wall of the hair.

Regarding the structure of **the petiole** a reference to Plitt's work is sufficient, since only fourteen genera have been investigated, so that the results cannot be of general importance.

The structure of the **axis**, like that of the leaf, requires further detailed investigation. The following facts concerning the structure of the **wood** in the woody species may be pointed out in accordance with Michael's work and the statements in my 'Holzstruktur[1].' The arrangement of the vessels and the size of their lumina, as well as the breadth of the medullary rays, are very variable. The broad medullary rays have a characteristic composition according to Michael. In tangential longitudinal section they consist of short (radially elongated) cells, which are surrounded, either partially or on all sides, by one or more layers of high cells; these are rather prosenchymatous in shape, and occasionally merge into the wood-prosenchyma. If we suppose the short cells to remain undeveloped, a xylem lacking medullary rays will result, and, according to Michael, this is actually found in *Santolina*, and also in *Ageratum*. A curious appearance of the wood in transverse section is presented by certain species of *Pteronia* (*P. camphorata*, L.); narrow radial strips of wood, consisting of vessels and prosenchyma, here alternate with broader strips of prosenchyma, enclosing the uniseriate medullary rays[2]. The size of the lumen of the vessels varies between ·02 and ·054 mm. in the species investigated by me; in the same way the diameter of the border of the pits of the vessels varies from ·002 to ·004 mm. All the species investigated by Michael and myself possess bordered pits, even on those portions of the vessel-wall which are in contact with parenchyma. Spiral striation of the wall of the pitted vessels has been observed to be more or less pronounced in certain species of *Ageratum, Artemisia, Athanasia, Baccharis, Eriocephalus, Euryops, Eupatorium, Gymnosperma, Helichrysum, Leucomeris, Pentzia, Proustia, Pteronia, Santolina, Staehelina, Stevia, Tarchonanthus, Vernonia*, and *Zaluzania*. The perforations of the vessels are generally simple; this is the case in the species named in my 'Holzstruktur,' in the thirty-two species investigated by Michael, and the thirteen (chiefly herbaceous) species examined by Tangl. Side by side with the simple perforations of the vessels scalariform perforations occasionally also occur, just as in the Rubiaceae. It is worthy of remark, that these scalariform perforations often have a circular contour, that they are often provided with very numerous bars, and that they also occur on horizontal division-walls between the constituent elements of the vessels. On those end-walls which are inclined from one radial wall of the vessel to the other, the (usually delicate) bars of the perforations are not always placed horizontally, as is normally the case elsewhere, but are occasionally in a vertical position. By branching and anastomosis of the bars, elegant patterns arise, such as Tangl has described in *Helianthus annuus* and *H. giganteus, Sonchus oleraceus, Ageratum*, and *Echinops exaltatus*. These scalariform vessel-perforations, which were first mentioned by Th. Hartig and Sanio as occurring in species of *Cichorium, Hieracium*, and *Onopordon*, and which I have found in species of *Albertinia, Berkheya, Calea, Cullumia, Lychnophora, Tripteris*, and *Zaluzania*, are, however, of no very great systematic interest. The wood-parenchyma is chiefly restricted to the neighbourhood of the vessels. The wood-prosenchyma, which forms the ground-mass of the wood, has simple

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[1] The former work deals with the following genera: *Ageratum, Amphiraphis, Artemisia, Baccharis, Barnadesia, Berkheya, Brachylaena, Centaurea, Chrysanthemum, Eurybia, Eupatorium, Gnaphalium, Helichrysum, Olearia, Oyedaea, Ozothamnus, Pentzia, Santolina, Senecio, Sonchus, Stevia, Tarchonanthus* and *Verbesina*; the statements in my 'Holzstruktur' are based on an investigation of species of the following genera: *Ageratum, Albertinia, Athanasia, Bahia, Berkheya, Calea, Cullumia, Eriocephalus, Euryops, Eupatorium, Gymnosperma, Leucomeris, Lychnophora, Osteospermum, Pluchea, Proustia, Pteronia, Raillardia, Staehelina, Tarchonanthus, Tripteris, Zaluzania*.

[2] Regarding the tissue of the medullary rays in this Order compare the detailed statements of Herbst (loc. cit.).

pits in all the species investigated. Septation of the wood-prosenchyma by means of fine division-walls has been observed in species of *Eupatorium, Raillardia, Senecio,* and *Verbesina.*

It is impossible to go into details here concerning the structural differences presented by the xylem of the vascular system in herbaceous species. As shown by Hildebrandt's investigations on this subject, in which the groups Ambrosiaceae and Senecionidae were dealt with, numerous differences occur, which will occasionally be of value in the diagnosis of species, if used with sufficient caution. Among these features are the varied (parenchymatous or prosenchymatous) differentiation of the interfascicular tissue, the presence or absence of medullary rays, &c.

There are very few statements regarding the structure of the **cortex** (see especially Vuillemin's work). The formation of the cork is superficial in the cases investigated. Douliot records subepidermal development of cork in species of *Achillea, Baccharis, Cosmophyllum, Ptarmica,* and *Tarchonanthus,* epidermal development in species of *Artemisia, Barnadesia,* and *Gaillonia.* According to Vuillemin, the cork also arises snbepidermally in *Hieracium* and *Scorzonera,* but epidermally in *Cacalia.* The primary cortex frequently contains collenchymatous tissue. Stone-cells have been observed in the primary cortex of *Stifftia chrysantha.* The endodermis is distinct in most cases, being characterized by Caspary's dots on the radial walls or by uniformly suberized walls or by its starchy contents. More rarely the endodermis is wanting. In *Barnad.sia rosea* the internal tangential and the radial walls of the endodermal cells become sclerotic, so that they appear to be thickened in the form of a horseshoe when seen in transverse section. The inner portion of the pericycle very frequently contains isolated primary bundles of hard bast, the cells of which are occasionally septate. Sclerenchymatous cells occasionally also appear in the bast; thus, according to Vuillemin, scattered bast-fibres are found in the secondary bast of *Achillea Ageratum* and small groups of bast-fibres in *Artemisia Abrotanum,* whilst in *Anthemis nobilis* and *Leontopodium alpinum* the entire bast-parenchyma becomes sclerotic. According to Vuillemin the sieve-tubes of the bast always have simple sieve-plates with pores of varying size.

In a number of species **anomalous structure of the axis** is found. According to H. Schenck, some of the .ianes belonging to this Order have normal structure, e.g. the species of *Piptocarpha.* On the other hand, Schenck has observed a furrowed xylem-mass, recalling the structure of the Bignonieae, in an undetermined member of the Order, which is shown in Figures 175, 176 of his Plate XII. The furrows in this xylem-mass are due to reduced activity on the part of certain longitudinal strips of the cambium, which leads to a smaller production of wood and a proportionally greater development of phloem externally; in this way the cambium becomes divided up into a number of strips, some of which are narrow and lie at the base of the furrows, while the others are broad, and are situated opposite the prominences of the wood. No splitting occurs in the medullary rays which limit the furrows laterally, contrary to the case of the Bignonieae; the tensions, which must arise in the course of secondary thickening, are compensated for by division and stretching of the cells of the medullary rays. In the stems of species of *Mikania* and of *Bidens rubifolius,* H. B. K., the *Aristolochia*-type of structure occurs; in these plants broad primary and secondary medullary rays divide the wood up into narrow plates. The formation of wedges of bast, as found in the Bignoniaceae, is occasionally associated with the former type, e.g. in *Bidens rubifolius* and in the stem of a *Mikania,* figured by H. Schenck on Plate XII, Fig. 178. In the last-named plant a third anomaly is to be found, for a secondary zone of growth (i.e. a broad zone of wood and bast) is situated on one side of the normal

ring of bundles; this zone probably originates in the pericyclic parenchyma of the vascular ring. An anomaly, similar to that last discussed, also occurs in *Kleinia spinulosa*, Hort. Petrop., according to Joh. Müller; here we have the formation of new secondary bundles of wood and bast, which apparently arise in the phloem of the original vascular ring; according to Kruch a similar anomaly is found in the basal part of the stem of *Dahlia imperialis*, in the endodermis of which secondary bundles of wood and bast, or of bast alone, originate. A somewhat different anomaly of the stem is present in *Coreopsis auriculata*, L., according to Hildebrandt. In the young stem of this plant a ring of bundles with rather strongly sclerosed interfascicular tissue is found. If I understand Hildebrandt rightly, the activity of the cambium in one or other of the primary vascular bundles ceases sooner or later; thereupon a new cambial arc, which forms wood internally and a little bast externally, arises on the outer side of the arc of primary hard bast belonging to the bundle in question; the masses of tissue, situated externally to the interfascicular tissue, also develop into a cambium, which becomes continuous with the newly formed cambial arcs, and so on. Another anomaly, which is very widely distributed amongst the Cichoriaceae, consists in the appearance of (*a*) medullary phloem-bundles or (*b*) medullary vascular bundles, owing to the addition of xylem to the phloem. These medullary bundles were first described by Hanstein and later by Trécul, and since then their presence in a considerable number of Cichoriaceae has become known especially through the work of Petersen and Kruch. Before proceeding to enumerate the genera in which these bundles have been observed, and those in which they are wanting, the following facts may be pointed out. The bundles in question are to be regarded as more or less reduced vascular bundles, as, according to J. E. Weiss, is evident from a consideration of their course [1]; they are branches of the peripheral ring of bundles, although, in some cases, only the outermost portions of a leaf-trace (i. e. the phloem) and not the entire strand (as in the formation of medullary vascular bundles) passes into the pith. Hence they only have the systematic value of medullary vascular bundles and when used in classification they are, generally speaking, only of importance for specific diagnosis. They are either confined to the margin, or are found both in the interior and at the margin of the pith, or they are irregularly distributed in this tissue. In those cases in which the bundles only consist of phloem and are situated at the margin of the pith, they sometimes give the appearance of bicollateral structure to the vascular bundles of the normal ring. The medullary bundles are usually simply collateral, rarely (lowest internodes of *Scorzonera hispanica*, L., according to J. E. Weiss, and of *Tragopogon pratensis*, L., according to Bergendal) concentric with central phloem. In many species the position and structure of the medullary vascular bundles is uniform throughout the stem; in other species, however, it varies in different regions.

Medullary bundles have been observed in species of *Crepis*, *Cymboseris*, *Dahlia*, *Helminthia*, *Hyoseris*, *Lactuca*, *Leontodon*, *Mulgedium*, *Picridium*, *Picris*, *Podospermum*, *Pyrrhopappus*, *Rodigia*, *Scolymus*, *Scorzonera*, *Sonchus*, *Thrincia*, *Tragopogon*, *Urospermum*; on the other hand, they have not been found in species of *Andryala*, *Apargia*, *Arnoseris*, *Barkhausia*, *Catananche*, *Chondrilla*, *Cichorium*, *Crepis*, *Endoptera*, *Geropogon*, *Hedypnois*, *Hieracium* [2], *Hypochaeris*, *Hyoseris*, *Kalbfussia*, *Koelpinia*, *Lactuca*, *Lampsana*, *Leontodon*, *Microseris*, *Mulgedium*, *Picridium*, *Picris*, *Prenanthes*,

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[1] In *Lactuca sativa* alone J. E. Weiss also met with small medullary phloem-bundles, which, as a consideration of their course shows, are equivalent to intraxylary soft bast; i. e. they form the continuation of phloem-bundles, which are found in the petiole internal to (above) the primary vessels.

[2] The statement regarding the occurrence of medullary vascular bundles in *Hieracium*, which has continually reappeared since Hanstein's time, is incorrect.

Pterotheca, Rhagadiolus, Robertia, Rodigia, Scorzonera, Seriola, Spitzelia, Taraxacum, Thrincia, Tolpis, Willemetia, Youngia, Zacintha, Zollikoferia. For details see Hanstein, Petersen, and Kruch, loc. cit.

Elsewhere than in the Cichoriaceae medullary phloem or vascular bundles have been met with in *Gundelia Tournefortii* (Trécul), *Helenium californicum* (Link), and *Obeliscaria pinnata*, Cass. (Hildebrandt)[1].

Cortical vascular bundles also occur in this Order, viz. in numerous species of *Centaurea* (for details see Heinricher, loc. cit.), in *Gundelia Tournefortii*, and also, according to Hildebrandt, in the wings of the stem of *Ammobium alatum* and *Helenium californicum*, and in *Senecio Doria*.

The development of the cortical vascular bundles in the species of *Centaurea* is correlated with the occurrence of a large amount of assimilatory tissue. *C. argentea*, L., *C. argophylla*, Steud., and *C. gymnocarpa*, have two kinds of shoots, the one with, the other without assimilatory tissue in the cortex; cortical vascular bundles are present in the first type of shoot only. The cortical bundles are usually normally orientated; occasionally, however, they are so placed that the xylem is external, or they may be reduced to xylem only. In *Centaurea regia*, Boiss., *C. gigantea*, *C. alata*, and *C. acaulis*, L. they are so numerous that the normal ring of bundles is rendered inconspicuous and the axis has a more or less distinctly monocotyledonous type of structure.

NOTE.—A few **anomalous structures in the root** must be added to the list of anomalies in the axis; these have been described by Dutailly. In *Taraxacum dens leonis*, *Cirsium lanceolatum*, and *Scorzonera hispanica* peculiar groups of cells are observed in a transverse section of the wood; they consist of a few centrally placed vessels filled with secretion, and are surrounded by a sheath of cambial tissue consisting of several layers. Similar cell-groups, containing a small, not readily recognized, secretory canal at their centre, and surrounded by a sheath of fibrous cells with an external ring of cambial tissue and then by a few tracheides, occur in the wood of the thicker roots of *Scorzonera hispanica*. The groups of cells in question are invariably secondary formations.

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[1] It may be remarked that in *Artemisia* and other allied genera a considerable multiplication of cells takes place in the peripheral portion of the pith, so that a kind of secondary pith arises, the cells of which are much elongated radially in the transverse section. Secondary cell-divisions also occur elsewhere in the pith, but never to such an extent as in *Artemisia*. (Hérail.)

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CANDOLLEACEAE (STYLIDIACEAE).

Up to the present time our knowledge of the anatomy of this Order has been essentially confined to the **anomalous stem-structure**, which Vesque first described as occurring in certain species of *Candollea* with elongated internodes (*Stylidium adnatum*, R. Br., *S. bulbiferum*, Benth., *S. cicatricosum*, Sond.,

S. dichotomum, DC., *S. fruticosum*, R. Br., *S.* '*lancifolium*[1],' *S. rhynchocarpum*, Sond.). In these species a transverse section of the stem shows a ring of isolated vascular bundles, which are few in number and slightly developed, and are united by interfascicular sclerenchyma; immediately adjoining this is a broad ring of fibre-like sclerenchyma, which encloses a few vessels and small phloem-groups[2] and extends as far as the endodermis (Fig. 105). According to Vesque and Van Tieghem, the ring of tissue just referred to originates through the activity of a secondary meristematic ring, which appears in the pericycle immediately internal to the endodermis, and forms sclerenchymatous fibres, vessels and phloem-groups on one side (the inner) only, and ultimately itself passes over into permanent sclerenchymatous tissue. In the root the same anomalous structure is found, and not only in *S. adnatum* and *S. dichotomum*, but also in species with a radical rosette of leaves (e.g. *S. graminifolium* and *S. spinulosum*), the stems of which show normal structure (Van Tieghem). According to Van Tieghem, *Forstera Bidwillii* and *F.* '*sedoides*[3],' as well as '*Phyllachne muscifolia*' (= *P. uliginosa* ex Syn.), also have stems with normal structure. In *Coleonema Preissii*, a rather broad ring of fibre-like sclerenchyma occurs on the inner side of the endodermis and adjoining the ring of vascular bundles; it, however, lacks vessels and bast-tissue, although, as in the previous cases, it may have originated from a secondary meristem. The perforations of the vessels are simple in *S. adnatum*.

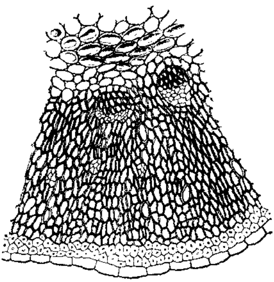

FIG. 105. Transverse section of a stem of *Stylidium adnatum*, R. Br. (extending from the pith to the endodermis).—Original.

I have investigated the **leaf-structure** in *Candollea alsinoides*, F. v. Müll., and *C. graminifolia*, F. v. Müll., *Levenhookia pauciflora*, Benth. and *Forstera* sp. (Helms, in Herb. Monac.). The stomata are irregularly surrounded by ordinary epidermal cells. They are found on both sides in *Candollea graminifolia*, only on the lower side in the remainder of the above species; in both species of *Candollea* they are arranged so that the pores are parallel to one another and to the longitudinal axis of the leaf. Special differentiation of the epidermis of the leaf is mentioned by Diels as occurring in *Phyllachne subulata*, F. von Müll.; the cells situated at the margin and in the median line of the leaf have extremely thick walls and are prosenchymatous.

Oxalate of lime has not been observed in this Order; on the other hand, nuclear crystalloids are found in the epidermis of the leaf and in the mesophyll (Zimmermann and Raunkjär). A hairy covering is found on the stem of *Levenhookia pauciflora*, in the form of short unicellular hairs, shaped like fingers, and glandular hairs with long multiseriate stalks and spherical heads composed of a few cells. In *Forstera* sp. peculiar cells with secretory contents occur in the lower epidermis of the leaf.

It remains to be mentioned, that the occurrence of **inulin** has been demonstrated in the genus *Stylidium* by G. Kraus.

[1] Annon sphalmate ex '*laricifolium*, Poir.'?

[2] Van Tieghem mentions that the secondary tissue of *S. adnatum* contains reduced vascular bundles; this does not quite agree with what has been said above.

[3] Annon sphalmate ex '*sedifolia*'?

Literature: G. Kraus, in Bot. Zeit. 1877, p. 329.—Vesque, in Ann. sc. nat., sér. 6, t. vii, 1878, pp. 204-8 and pl. 17.—Van Tieghem, in Bull. Soc. bot. de France 1883, p. 308 and 1884, p. 164.—Van Tieghem and Morot, in Ann. sc. nat., sér. 6, t. xix, 1884, pp. 281-6 and pl. 13.—Schönland, in Nat. Pflanzenfam., iv. Teil, Abt. 5, 1889, pp. 80-1.—Zimmermann, Pflanzenzelle, 2. Heft, 1891, p. 126.—Diels, in Engler, Bot. Jahrb., Bd. xxii, 1896, p. 255.

GOODENIACEAE.

The anatomy of the Goodeniaceae is still incompletely known. An important feature, in consideration of their close affinity with the Lobeliaceae, is the absence of laticiferous tubes, but inulin has been shown to occur in the genera *Goodenia*, *Selliera*, *Euthales*, and *Scaevola* by G. Kraus.

The **structure of the leaf** has been investigated by me in *Goodenia ovata*, Sm., *Selliera radicans*, Cav., *Scaevola Lobelia*, Murr., and *Dampiera Brownii*, F. v. Müll., and by Briquet in *Brunonia*. The stomata, which occur either on the lower surface only (*Goodenia ovata*, *Dampiera Brownii*), or on both surfaces of the leaf, are surrounded by a varying number of epidermal cells without distinctive shape in the species examined by me, whilst in *Brunonia* they are surrounded by four subsidiary cells, two of which lie parallel to the pore, while the other two are applied to the narrow ends of the pair of guard cells. The leaf-structure is typically bifacial (e.g. in *Dampiera Brownii*), but is centric in *Scaevola Lobelia*. The mesophyll of *Brunonia* is peculiar, its cells being elongated parallel to the surface of the leaf. The vascular bundles of the veins are surrounded by a suberized sheath in *Goodenia ovata*; they are supported by a sclerenchymatous arc in *Selliera radicans*, whilst in *Dampiera Brownii* both sheath and sclerenchyma are wanting. Hair-like sclerenchymatous cells, branched like an Ophiurid, have been observed in the mesophyll of numerous species of *Dampiera* by O. Bachmann; silicified groups of cells, in the formation of which both epidermal and subjacent mesophyll cells take part, have been observed in *Dampiera Brownii*. I have met with oxalate of lime in the form of small crystalline bodies in the mesophyll of *Goodenia* and *Dampiera*. Both clothing and glandular **hairs** are found. The former include the very short unicellular sclerenchymatous hairs of *Goodenia ovata*, the simple uniseriate hairs of *Brunonia* and peculiar hairs resembling a fir-tree, and occurring in *Dampiera Brownii* (Fig. 106, *A–B*). The upper portion of the trichomes last mentioned consists of unicellular, shortly-stalked, two-armed hairs with equal arms, which are placed one above another, in such a way that the arms of successive tiers never fall into the same vertical plane, but intersect one another at an acute angle [1]. The glandular hairs in *Goodenia ovata* and *Scaevola Lobelia* are shortly stalked peltate glands, the shield of which consists of a few cells separated by radial walls; it is slightly lobed at its margin owing to the convex projection of the component cells; on the other hand, *Calogyne Berardiana*,

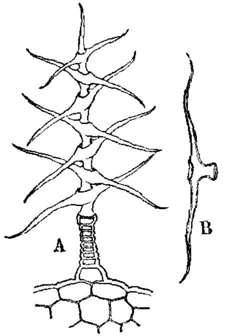

FIG. 106. Trichomes of the Goodeniaceae: A, B, hair resembling a fir-tree and belonging to *Dampiera Brownii*, F. v. Müll.; B, a single cell forming one tier of the same.—Original.

[1] 'Stellate hairs' are stated by systematists to occur in *Scaevola* and *Verreauxia* besides *Dampiera*; their structure is unknown.

F. v. Müll. has glandular hairs with a uniseriate stalk and an ellipsoidal head made up of a few cells.

Concerning the anatomy of the **wood** the following facts may be quoted from the statements in my 'Holzstruktur[1]': the vessels have simple perforations and bordered pitting where they are in contact with parenchyma of the medullary rays. The wood-parenchyma is only slightly developed. The medullary rays are usually one or two, rarely as much as four cells in breadth, and are elongated in the vertical direction. The wood-prosenchyma[2] has bordered pitting.

With regard to the structure of the **cortex**, Vesque's observations have shown that the primary cortex of *Goodenia ovata* and *Scaevola Plumieri* is lacunar, and that the periderm arises subepidermally in *Scaevola*, whilst pericyclic development of cork is known through Briquet's work to occur in the rhizome of *Brunonia*.

In some species **anomalous stem-structure** occurs, consisting essentially in the appearance of medullary vascular bundles. This has been investigated in the greatest detail in *Goodenia ovata* by Vesque. A transverse section through an internode of the stem (Fig. 107) of this species shows five (medullary) vascular bundles on the inner side of the peripheral vascular ring, which is closed owing to the formation of interfascicular wood; these bundles have normally developed bast on

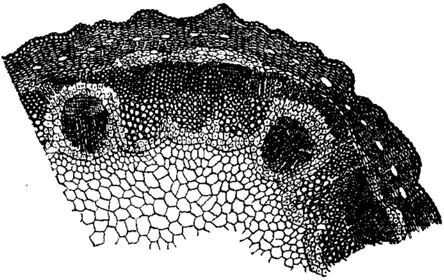

FIG. 107. Diagrammatic transverse section of the anomalous axis of *Goodenia ovata*, Smith.—Original.

the outside and penetrate more or less deeply into the peripheral ring of wood and bast, which is far less strongly developed at these points than elsewhere. The medullary vascular bundles are further separated from the peripheral xylem-ring by a medullary sheath composed of septate prosenchyma, which has thick walls, rather wide lumina and simple pits, and sometimes entirely surrounds the medullary bundles. Vesque has shown that these medullary vascular bundles are leaf-traces, which subsequently pass into the peripheral ring of bundles. In addition to *G. ovata*, Vesque only found them in *G. heterophylla*, Sm., among the numerous species of *Goodenia* examined by him; and among other members of the Order[3] he only met with them in *Selliera radicans*, Cav., and '*Distylis*' (= *Calogyne*, R. Br.)[4].

[1] Species of *Goodenia*, *Scaevola*, and *Dampiera* were investigated.
[2] The tissue of the medullary sheath of *Goodenia* (see below) does not belong to the wood-prosenchyma.
[3] Besides the above Vesque examined species of *Dampiera*, *Leschenaultia*, *Scaevola*, and *Velleia*.
[4] *Distylis Berardiana*, Gaud. = *Calogyne Berardiana*, F. v. Müll. is probably intended.

Literature: Vesque, Anat. comp. de l'écorce, Ann. sc. nat., sér. 6, t. ii, 1875, p. 146 and pl. 10 and Anat. du *Good. ovata*, loc. cit., sér. 6, t. iii, 1876, pp. 312–26 and pl. 19.—G. Kraus, in Bot. Zeit. 1877, p. 329 (see also Sitz.-Ber. Halle'sch. Naturf.-Vers. 1875).—Solereder, Holzstr., 1885, pp. 158–9 —O. Bachmann, in Flora 1886, separate copy, p. 18.—Schönland, in Natürl. Pflanzenfam., iv. Teil, Abt. 5, 1889, p. 71 (anomaly of *Goodenia* incorrectly interpreted).—Briquet, *Brunonia*, Bull. de l'Herbier Boissier, t. iv, 1896, pp. 317–23.—Warming, Halofyt Stud., K. Danske Vid Selsk. Skr. 1897, p. 209.

CAMPANULACEAE (incl. LOBELIACEAE).

The occurrence of inulin and laticiferous vessels in this Order constitutes an approach from the anatomical point of view to the Compositae and more especially to the Cichoriaceae, which the Campanulaceae resemble in other respects.

Since Prantl discovered inulin in *Campanula rapunculoides*, it has been shown to occur in a number of genera[1] by G. Kraus. The **laticiferous tubes** of the Campanulaceae[2] have been especially examined by Trécul. In the axis the chief seat of their occurrence is the inner region of the phloem (i.e. the part nearest the xylem of the vascular bundle). In many cases they are not to be found in the periphery of the phloem-groups or in the primary cortex (species of *Adenophora, Campanula, Lobelia, Phyteuma*) or they are only of isolated occurrence; in other cases, however, they occur abundantly (species of *Centropogon, Isotoma, Lobelia, Musschia, Piddingtonia, Siphocampylus, Tupa*). In the latter case they sometimes extend as far as the epidermis (*Musschia aurea, Tupa Feuillei*, &c.) and in one species (*Siphocampylus manettiaeflorus*) they even penetrate it and form small papillae on the surface of the branch. In those species which possess medullary vascular or phloem-bundles (see below), the laticiferous tubes are also to be found in the soft bast of these bundles. They have not been observed in the xylem or pith in the Campanulaceae sens. str. nor in most of the Lobeliaceae. In other Lobeliaceae (e.g. *Centropogon surinamensis, Lobelia syphilitica, Siphocampylus manettiaeflorus, Tupa salicifolia*) Trécul met with them in the peripheral part and occasionally also in the interior of the pith, and these medullary laticiferous tubes were found to be connected with those in the cortex by means of branches, traversing the xylem-ring. In the leaf the laticiferous tubes occur in the veins, being generally (*Campanula grandis, Centropogon surinamensis, Tupa salicifolia*, &c.) situated on the lower side, more rarely (*Campanula rapunculoides, Lobelia laxiflora*, &c.) on the upper side of the vascular bundles; they are also, but not always, found free in the mesophyll (e.g. in *Canarina campanulata* and species of *Campanula*; but not in *Jasione montana*). E. Schmidt has demonstrated the occurrence of a protoplasmic body and of nuclei in the laticiferous tubes.

The **leaf-structure** has been examined in a general comparative manner by Vesque and presents no special features. It is important that the stomata are not surrounded by any special subsidiary cells, but by a varying number of irregularly arranged epidermal cells; the initial cell divides by one or by several curved and variously orientated division-walls. Large water-pores appear always to occur on the upper surface of the glands which terminate the leaf-teeth and are developed even on the cotyledons. Oxalate of lime has not been observed. The sphere-crystals, which Baccarini met with[3] in alcohol-material

[1] These are: *Adenophora, Campanula, Centropogon, Isolobus, Isotoma, Lobelia, Michauxia, Musschia, Phyteuma, Pratia, Siphocampylus, Symphyandra, Trachelium, Tupa.*

[2] Laticiferous tubes have hitherto only been demonstrated in a small number of the genera (*Adenophora, Campanula, Canarina, Centropogon, Isotoma, Lobelia, Musschia, Phyteuma, Piddingtonia, Siphocampylus* and *Tupa*); but the statements of systematists lead one to assume a wide and perhaps universal distribution.

[3] Nuclear crystalloids have been demonstrated in the palisade-tissue of species of *Campanula* (Zimmermann, Pflanzenzelle, Heft 1, 1890, p. 72 and Heft 2, 1891, p. 127).

of *Campanula Cervicaria*, L., *Trachelium coeruleum*, L., and *Specularia Speculum*, A. DC., must not be confounded with oxalate of lime. As regards the **hairy covering** it may be pointed out that glandular hairs are wanting. The clothing hairs are unicellular and occasionally silicified, as first mentioned by De Bary in the case of *Campanula Cervicaria* and by Wettstein in *Hedraeanthus*. Heinricher has described peculiar reduced forms of hairs as occurring in *Campanula persicifolia*, *C. grandis*, Fisch. et Mey., and *C. patula*, L. In these species the hairs are reduced to quite small, solid, conical lumps, which are brittle and hence easily broken off, and only project slightly beyond the level of the outer wall of the epidermis; at the same time a cystolith-like peg of membrane, which is often distinctly stratified, projects from the outer wall into the lumen of the cell; both this and the external knobs are silicified. Vesque observed similar 'cystolith'-hairs, in which he also records a calcification of the membrane; while H. Schenck describes a delicate skeleton of carbonate of lime in the long simple unicellular hairs of *Campanula medium*, which have a verrucose surface.

In the structure of the **axis** the anomalous features have formed almost the sole subject of investigation; they consist in the occurrence of medullary vascular bundles and phloem-strands, and of cortical bundles. Before passing on to discuss these, I will communicate the little that is known of the remaining features of wood and cortex. According to Douliot, internal cork-formation (in the pericycle) takes place in the subterranean axes of *Tupa ignescens* and *Campanula alata*. I have investigated the structure of the wood in detail in *Siphocampylus duploserratus*, Pohl, *Roella ciliata*, L., and *Lightfootia tenella*, DC. (Strasburger in *Campanula Vidalii*). The transverse section of the wood in these species shows vessels of no great diameter (up to ·045 mm.) and medullary rays which may be as much as four cells in breadth (*Siphocampylus*). The perforations of the vessels are simple and mostly elliptical, occasionally elongated-elliptical (*Siphocampylus*); in *Roella* and *Lightfootia* scalariform perforations with few bars are also found in small numbers. The vessels have bordered pits on their walls, including those which are in contact with the tissue of the medullary rays. The wood-prosenchyma of *Siphocampylus* has simple pits, and is occasionally septate; on the other hand, in *Roella* and *Lightfootia* the wood-prosenchyma has bordered pits. The wood-parenchyma is developed in some abundance in *Lightfootia* only.

The **medullary phloem and vascular bundles**, of which I am now about to speak, have been observed in the genera *Campanula*, *Hedraeanthus*, *Michauxia*, *Phyteuma*, and *Symphyandra*. They do not, however, occur in all, but only in certain species of these genera[1]. Their systematic importance depends solely on their occurrence or absence in individual species; their detailed structure and their number sometimes vary considerably in the same species, as Petersen's and J. E. Weiss's investigations have shown. The leaf-trace nature of these bundles has been demonstrated in species of *Campanula* by J. E. Weiss. Westermaier brings the occurrence of these bundles in the genus *Campanula* into relation with the abundance of flowers, because medullary bundles are not to be found in any species which has few flowers, as long as the height attained by the plant is small. This law is based on the investigation of fifty-four species and is thoroughly intelligible on physiological grounds relating both to the nutrition and the mechanics of the plant, but the converse

[1] The anomaly in question has been observed in the following Campanulaceae (sens. str.) according to Petersen, Westermaier, Hérail and others: *Campanula alliariaefolia*, *C. bononiensis*, *C.* '*Calcitrapa*,' *C. Cervicaria* (according to Trécul contrary to Hérail), *C. crispa*, *C. divergens*, *C. glomerata*, *C. Grossekii* (according to Petersen contrary to Hérail), *C. interrupta*, *C. lamiifolia*, *C. latifolia*, *C. macrantha*, *C. multiflora*, *C. pendula*, *C. petraea*, *C. pyramidalis*, *C. rhomboidea*, *C. ruthenica*, *C. sarmatica*, *C. Trachelium*; *Hedraeanthus* sp.; *Michauxia campanuloides*; *Phyteuma limonifolium*; *Symphyandra pendula*.

does not hold good, since tall species with many flowers, such as *C. rapunculoides*, L. and *C. medium*, L., may have normal structure.

The following statements regarding the varied differentiation of the medullary vascular bundles and phloem-strands within the genus *Campanula* are derived from the works of Petersen and J. E. Weiss. In *Campanula latifolium* and *C. Trachelium*, according to Petersen, isolated bundles of soft bast are found at the outer margin of the pith; in the first-named species they are only separated from the xylem of the normal ring by a few layers of cells, and in the other species they come into still closer connexion with the normal vascular bundles, so that the latter appear to have bicollateral structure. According to Petersen *C. divergens* possesses similar medullary bundles of soft bast, some of which are, however, in this case accompanied by rudimentary xylem-groups. In this way a transition is established to the structure of other species of *Campanula* (such as *C. alliariaefolia, C. glomerata, C. lamiifolia, C. pyramidalis*, also—see above—*C. latifolia*, according to J. E. Weiss), in which vascular bundles are present in the pith. These medullary vascular bundles, which occur especially in the peripheral part of the pith, are collateral and inversely orientated in the simpler cases; their xylem is external, their bast internal. Occasionally (e.g. in *C. latifolia*) they are isolated, but they frequently (e.g. in *C. glomerata*) coalesce to form a closed ring of bundles. In other cases (e.g. *C. sarmatica*) concentric vascular bundles with central phloem and peripheral xylem occur, and, probably by the fusion of such strands, medullary strips and rings of bundles arise; these exhibit a band of soft bast in the middle and both externally and internally to this a strip of xylem. All these internal vascular bundles have cambial tissue between wood and bast, whether the bundles are isolated or fused together. In the case just mentioned, in which groups of bundles with a central band of phloem and two peripheral bands of wood occur, there are also two cambial layers present in the normal positions. With regard to the other genera it may be mentioned that *Michauxia campanuloides* has one, *Phyteuma limonifolium* two rings of inversely orientated vascular bundles in the pith.

In connexion with the discussion of the medullary vascular bundles we may shortly refer to the occurrence of medullary cork in relation to the medullary bundles, as was observed by Hérail. In *Campanula pyramidalis* a cork-cambium forming cork internally arises on the inner side of the bundles, which are arranged in a ring and are inversely orientated; in *Phyteuma limonifolium* the formation of cork takes place at the periphery of the central medullary ring of bundles. The development of cork in the pith of the stem has not been observed in any Order other than the Campanulaceae.

Cortical vascular bundles have been observed by J. E. Weiss in *Campanula pyramidalis*, and by Bower in *Lobelia rhynchopetalum*, Hemsley.

The cortical bundles of *Campanula pyramidalis* are of the nature of leaf-traces; they are 3–5 in number, and are perhaps always composed of two or more vascular bundles; they are concentric with central xylem and possess a cambium. In appearance they are not unlike the peripheral rings of vascular bundles of certain Serjanieae. According to Bower, the accessory cortical bundles in *Lobelia rhynchopetalum*, a palm-like plant, are not of the nature of leaf-traces, but arise from strands of secondary meristem in the primary cortical parenchyma. The individual strands have central xylem and peripheral bast, and increase in thickness by cambial activity. Their course is not vertical, i.e. in the direction of the axis, but is oblique to the latter; in their entirety they form a network, which is also connected with the leaf-trace strands, passing directly into the normal ring of bundles. On the whole, the system of cortical bundles of *Lobelia rhynchopetalum* reminds one of analogous structural features in the genus *Cycas*, and the shoot of the *Lobelia* in its different parts so closely resembles that of the latter genus, that if found in the fossil state it could scarcely be distinguished from a *Cycas*.

Literature: Hanstein, Milchsaftgef., Berlin, 1864, pp. 13 and 74 et seq.—Sanio, in Bot. Zeit. 1865, p. 179.—Dippel, Milchsaftgef., Rotterdam, 1865.—Trécul, Lact. dans les C., Compt. rend., t. lxi, 1865, p. 929 et seq. and Adansonia, t. vii, pp. 174–82.—De Bary, Vergl. Anat., 1877.—G. Kraus, in Bot. Zeit. 1877, p. 328.—Schmalhausen, Milchsaftbeh., Mém. de l'Acad. d. sc. de St.-Pétersbourg, sér. 7, t. xxiv, n. 2, 1877, pp. 22–5.—Westermaier, Abnorm. Dic.-Typus, Sitz.-Ber. Berliner Akad. 1881, pp. 1064–9.—E. Schmidt, Plasmak. d. gegl. Milchr., Bot. Zeit. 1882, pp. 444, 445.—Petersen, in Engler, Bot. Jahrb., Bd. iii, 1882, pp. 387–92.—Bower, Struct. of the stem

of *Rhynchopetalum montanum*, Journ. Linn. Soc., vol. xx, 1883, pp. 440–6, pl. 36–8.—J. E. Weiss, Markst. Gefässbündelsyst., Bot. Centralbl. 1883, iii, pp. 325, 358 and 401 et seq. and Tab. i.—H. Schenck, Wandverd. an Pfl.-Haar., Diss., Bonn, 1884, p. 23.—Vuillemin, in Bull. Soc. bot. de France 1884, p. 266.—Heinricher, Reduc. Org. bei Camp. etc., Ber. deutsch. bot. Gesellsch. 1885, pp. 4–13 and Tab. ii.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. i, 1885, pp. 221–3.—Hérail, Tige d. Dic., Ann. sc. nat., sér. 7, t. ii, 1885, pp. 290–3 and pl. 20.—Solereder, Holzstr., 1885, pp. 159, 160.—Pirotta e Marcatili, Vasi laticiferi etc., Ann. R. Ist. bot. di Roma, Anno ii, 1886, n. 2; abstr. in Just 1886, i, p. 922.—Volkens, Aegypt.-arab. Wüste, 1887, pp. 129, 130.—Wettstein, Monogr. v. *Hedraeanthus*, Denkschr. Wiener Akad. 1887, p. 185 et seq.—Douliot, in Ann. sc. nat., sér. 7, t. x, 1887, p. 382.—Baccarini, Sferocristalli, Malpighia ii, 1888–9, p. 9.—Dehmel, Milchsaftbeh. etc., Diss., Erlangen, 1889, p. 18 et seq.—Schönland, in Natürl. Pflanzenfam., iv. Teil, Abt. 5, 1889, pp. 41, 42.—Seligmann, Anat. Bezieh. d. C. etc., Bot. Centralbl. 1890, iii, pp. 1–5 (very unclear statements!).—Strasburger, Leitungsbahnen, Jena, 1891, p. 327.—Herbst, Markstr. Bot. Centralb. 1894, i, p. 404.—Grevillius, in Engler, Bot. Jahrb., Bd. xxiii, 1896, p. 73.—Russell, Climat méd., Ann. sc. nat., sér. 8, t. i, 1895, p. 342.

VACCINIACEAE.

This Order is distinguished anatomically by a tendency to form scalariform perforations in the vessels, by internal development of cork, by the occurrence of clothing and glandular hairs (for the latter see Fig. 108), and by the stomatal apparatus, which consists of a pair of guard-cells with a single subsidiary cell on each side, and placed parallel to the pore. The wood-prosenchyma has simple and bordered pits. Oxalate of lime is excreted in the form of clustered or solitary crystals. Special internal secretory receptacles are wanting. Of all the features mentioned above, the stomatal apparatus is the only one which distinguishes this Order from the very closely related Ericaceae.

The details of the leaf-structure have been examined more especially by Niedenzu[1], and the following statements are based principally on his work. The **cuticle** exhibits very great variation both as regards thickness and consistency. In the first place all transitions are found from quite a thin cuticle, as in *Vaccinium erythrocarpum*, Michx., to one of considerable thickness, as in the species of *Psammisia*. Where a thick cuticle occurs it is either soft, as in *Agapetes*, or may be hard and even stony, as in most of the Thibaudieae. All these features can be made use of for special anatomical diagnosis, if the necessary caution is exercised. Thus almost all the Thibaudieae are characterized by a thick and hard cuticle; the Vaccinieae of the sections *Oxycoccoides*, *Euvaccinium*, and *Cyanococcus* have, without exception, a thin or only slightly-thickened cuticle, and the Vaccinieae of the sections *Vitis Idaea* and *Neurodesia* have a well-developed cuticle. In the Thibaudieae the cuticle is very frequently provided with a scaly covering of wax; in a similar way the leaf-surface of *Vaccinium angustifolium*, Benth., has a white bloom owing to excretion of wax. The occurrence of cuticular ridges is another peculiarity of the cuticle, occasionally appearing in this Order. Apart from the cuticle the **epidermis** of the upper side of the leaf shows a whole series of anatomical features, most of which can be shown to be correlated with the nature of the habitat; they are mostly of importance for the diagnosis of species only. In the case which we will take first, the epidermis of the upper side of the leaf is simple and commonly consists of flat cells with thin straight or undulated lateral walls, as, for instance, in the Vaccinieae of the section *Euvaccinium*, further in *V. pensylvanicum*, Lam., *V. canadense*, Kalm, and *V. erythrocarpum*, Michx. In the Vaccinieae of

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[1] In Engler, Bot. Jahrb., Bd. xi, 1889. Niedenzu investigated the following genera: (*a*) in the tribe Thibaudieae: *Cavendishia*, *Ceratostemma*, *Eurygania*, *Semiramisia*, *Hornemannia*, *Macleania*, *Psammisia*, *Satyria*, *Disterigma*, *Thibaudia*, *Themistoclesia*, *Sophoclesia*, *Sphyrospermum*; (*b*) in the tribe Euvaccinieae: *Gaylussacia*, *Vaccinium*, *Agapetes*, *Pentapterygium*, *Oxycoccus*. The delimitation of both tribes is here taken as defined by Niedenzu (not as in Durand's Index) and the names of the two tribes are used in the same sense in the text above.

the section *Cyanococcus*, and in *Gaylussacia*, the epidermal cells likewise have thin walls, but are high; they serve as water-reservoirs and accordingly show a bellows-like folding of their lateral walls. The epidermal cells of the upper side are of a palisade-like shape, and have thick walls in *Vaccinium Moritzianum*, Klotzsch, *V. polystachyum*, Benth., and generally in the section *Vitis Idaea*, as well as in *Oxycoccus macrocarpus*, Pers. *Gaylussacia pinifolia*, Ch. et Schl., and *Satyria Warszewiczii*, Klotzsch, again are distinguished by quite a special type of differentiation of the upper epidermis. In the first of these two species the walls of the epidermal cells are provided with a spiral or reticulate thickening. *Satyria Warszewiczii*, Klotzsch, has epidermal cells which have almost the appearance of stone-cells in surface view; the thickening and pitting of the wall here extends to the internal walls (i.e. those parallel to the leaf-surface) and also to the lateral walls. In other members of the Order, a **hypoderm** is developed beneath the epidermis on the upper side of the leaf. It consists of one or more layers and its walls are also variously differentiated. In *Vaccinium coriaceum*, Miq., and in several species of *Disterigma*[1], a one-layered hypoderm is found beneath the upper epidermis; its walls are not specially thick and its cells exceed those of the epidermis in volume. In other cases the internal walls (i.e. those parallel to the leaf-surface), as well as the lateral walls of the one-layered hypoderm, are strongly thickened: this is the case in by far the greater number of the Thibaudieae investigated by Niedenzu (*Macleania*, *Psammisia*, *Euryganta*, *Ceratostemma*, *Cavendishia*, &c.). A similar strong thickening of the internal cell-wall (i.e. that parallel to the leaf-surface) is shown by the innermost cell-layer of the many-layered hypoderm of *Psammisia nitida*, Klotzsch. Finally, in some cases, a hypoderm of several layers of cells with thin walls occurs; it is recorded by Niedenzu as consisting of one or two layers in '*Vaccinium polyanthum*, Miq.' and several species of *Disterigma*, and of at least two layers throughout in other species of *Disterigma*, in *Satyria Warszewiczii*, Klotzsch and *S. clonantha*, Klotzsch (in Niedenzu's work '*chlorantha*' by a slip), as well as in *Thibaudia floribunda*, Bl. The **stomata**, as has already been stated above, are always accompanied by two subsidiary cells, placed parallel to the pore. As a rule, the stomata are only found on the lower surface of the leaf. Niedenzu met with them on the upper side in *Vaccinium erythrocarpum*, Michx., and occasionally also in *V. Myrtillus*. A further noteworthy feature in the structure of the epidermis is the absence in the Vacciniaceae of the gelatinization of epidermal or hypodermal cell-membranes, which occurs in the Ericaceae.

The **mesophyll** likewise presents various structural features. In the simplest case a differentiation into palisade and spongy tissue is scarcely indicated, the mesophyll consisting of thin-walled, almost isodiametric parenchymatous cells, e.g. in the species belonging to the sections *Euvaccinium* and *Cyanococcus* of the genus *Vaccinium*. In other cases the leaf-structure is bifacial, in others again centric. Other structural differences are connected with the thickness of the walls of the mesophyll-cells. A portion of these cells is commonly distinguished by having thick walls, while the remainder of them have thin walls; these latter take part in the storage of water and occasionally show a concertina-like folding of their walls, which may be regarded as an indication of such a function. In the species of *Vaccinium*, belonging to the section *Vitis Idaea*, there is a tendency for all the cell-walls of the assimilatory system to become uniformly thickened; in *Macleania Humboldtiana*, Kl., the uppermost palisade-layer has thin, the remainder of the mesophyll thick walls; in *Themistoclesia pendula*, Kl., the outer portion of the

[1] *Disterigma* is the section *Disterigma*, Klotzsch of the genus *Vaccinium*, which Niedenzu raised to generic rank.

mesophyll has thick, the inner portion thin walls, and so on. The structure of the mesophyll of *Sophoclesia nummulariaefolia*, Kl., deserves special notice in this connexion; here the uppermost palisade-layer, which contains scanty chlorophyll, consists of thin-walled cells, ½ mm. in height (which dwindle to $\frac{1}{20}$ mm., by concertina-like folding of their lateral walls, on the withdrawal of water); the next following layers of cells successively decrease in size, contain more chlorophyll and have thicker walls; so that they are progressively more and more adapted to assimilatory functions. The successive degrees of thickening of the lateral walls in the varions layers is attained in a curious manner; the cells of the second palisade-layer are stiffened by band-shaped strips of thickening, placed parallel to the leaf-surface, and in the succeeding cell-layers the number of unthickened strips of wall continually decreases. *Sophoclesia major*, Benth. et Hook., has the same differentiation of the first palisade-layer as *S. nummulariaefolia*; the remainder of the mesophyll, however, is uniformly thick-walled. The occurrence of stone-cells in the spongy tissue of *Cavendishia melastomoides*, Benth. et Hook., remains to be mentioned.

The vascular bundles of the **veins** are usually circular in transverse section and are embedded. Niedenzu has met with bundles of sclerenchymatous fibres

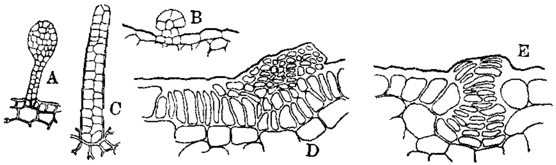

FIG. 108 Glandular hairs of the Vacciniaceae: A, *Vaccinium Vitis Idaea*, L.; B, *V. resinosum*, Ait.; C, *Macleania cordata*, Van Houtte; D, E, *Vaccinium ellipticum*, Miq.—After Niedenzu.

('marginal bast') in the margin of the leaf of *Vaccinium Vitis Idaea*, and some of the Thibaudieae.

The **trichomes** present are clothing and glandular hairs. The former are either simple unicellular hairs, which vary in length and in the thickness of their walls (in both tribes), or are simple uniseriate hairs (frequent amongst the Euvaccinieae). The glandular hairs may be referred to three types. To the first belong the glandular hairs of *Gaylussacia*. The stalk of these hairs is multiseriate throughout, or at least basally, and may be either long or short; in the first case the head, which does not consist of a very large number of cells, is small, in the second case it is large. The second type is formed by the glandular hairs of *Vaccinium* and *Oxycoccus*, where the stalk, which is almost invariably biseriate, and the multicellular head, which is composed of isodiametric cells, are of about equal length (Fig. 108, *A–B*[1]). Finally, the third type is represented by the narrow, tongue-shaped, glandular hairs of *Vaccinium*, sect. *Epigynium*, of *Agapetes*, and all the Thibaudieae (Fig. 108, *C–E*). These show no differentiation into stalk and head, and consist mostly of two, in *Epigynium* and *Agapetes* of three or more, rows of isodiametric cells. These tongue-shaped, glandular hairs are nearly always bent over towards the apex of the leaf in a direction

[1] Similar external glands cause the 'glandular' nature of the leaf-teeth of *Vaccinium Myrtillus* (Reinke).

parallel to that of the midrib, are often firmly adpressed to the epidermis, and fuse with it in their lower portions or occasionally throughout their entire length.

Oxalate of lime is excreted in the leaf in the form of clustered and solitary crystals. The former have the wider distribution. According to Niedenzu, solitary crystals are characteristic of the generic section *Euvaccinium*, clustered crystals of the sections *Vitis Idaea*, and *Cyanococcus*.

Little is known concerning the structure of the **axis**. The development of cork takes place in the pericycle in *Vaccinium* internally to the primary bast-fibres (Douliot, Maury). According to Simon, the bast-fibres are provided with bordered pits, as in the Ericaceae. The structure of the wood was investigated by me in *Thibaudia longifolia*, H. B. K., *Pentapterygium rugosum*, Hook. f., *Gaylussacia brasiliensis*, Meissn., and *Vaccinium uliginosum*, L. The numerous vessels of the wood have no great diameter in these species (maximum diameter = ·024 – ·045 mm.). The medullary rays are usually three-seriate and less, in *Thibaudia* as much as six cells in breadth. The perforations of the vessels vary. *Gaylussacia brasiliensis* has scalariform perforations only (with 2–14 bars); similarly *Vaccinium Myrtillus*, L., according to Chalon. In *Pentapterygium rugosum*, *Thibaudia longifolia* and *Vaccinium uliginosum*, scalariform and simple perforations are present side by side, the latter often having an elongate-elliptical outline; in the last-named species, moreover, perforations of a special kind are found, since the division wall of the vessel is traversed by very numerous small round pores (Fig. 109). Spiral thickening of the vessel-wall has been observed in the above-mentioned species of *Thibaudia*, *Pentapterygium*, and *Gaylussacia*, as well as in *Vaccinium Myrtillus*. Where in contact with parenchyma, the vessel-wall in *Pentapterygium* usually bears large simple pits, in the rest of these plants bordered pits. The wood-parenchyma is little developed. In a small number of cases the wood prosenchyma is provided with simple pits, but mostly bordered pits are found; the lumen of the wood-prosenchyma bearing simple pits is commonly septate by means of delicate transverse walls. The pith is homogeneous in the species of *Vaccinium*, *Oxycoccus*, and *Macleania*, investigated by Gris.

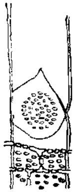

FIG. 109. Perforation in a vessel of *Vaccinium uliginosum*, L.—Original.

Literature: Gris, Moelle, Nouv. Arch. Mus. d'hist. nat., t. vi, 1870, pp. 250–1.—Reinke, Sekretionsorg., Pringsheim Jahrb., Bd. x, 1876, p. 157.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. 1, 1885, pp. 240–4.—Solereder, Holzstr., 1885, pp. 160–1.—Maury, Struct. des *Vaccinium* etc., Journ. de bot., t. i, 1887, pp. 104 and 115 et seq.—Douliot, in Ann. sc. nat., sér. 7, t. x, 1889, pp. 373–4.—Niedenzu, Anat. Bau d. Laubbl. d. Arbutoideae u. Vaccinioideae etc., Engler, Bot. Jahrb., Bd. xi, 1890, pp. 134 and 177 et seq., tab. iv–vi.—Simon, Vergl. Anat. d. Epacrid. u. Ericac., Engler, Bot. Jahrb., Bd. xiii, 1891, pp. 15–46 and Tab. ii.

ERICACEAE.

1. REVIEW OF THE ANATOMICAL FEATURES. This Order possesses only a few prominent characters common to all its members. A special point of difference from the Vacciniaceae lies in the fact that the stomata are surrounded by several epidermal cells in nearly all cases (excepting *Diplycosia* and a few species of *Gaultheria*). Special secretory receptacles are wanting, as in the Vacciniaceae. The Ericaceae, like the Vacciniaceae, have a tendency to the formation of scalariform perforations in the vessels, but simple perforations are also to be found accompanying the scalariform type; the mechanical tissue of the xylem consists principally of wood-prosenchyma with bordered pitting. The vessels generally have small lumina and their walls are provided with small bordered pits. It still remains to be determined whether the internal develop-

ment of cork, observed in this Order, as well as the bordered pitting of the bast-fibres, mentioned by Simon, is characteristic of all the species. The leaves usually have bifacial structure. Oxalate of lime is excreted in the form of clustered or solitary crystals. The hairy covering is very varied (Fig. 110). The clothing hairs include simple unicellular or uniseriate hairs, tufted hairs (*Clethra*), abietiform hairs (*Rhododendron*), and multiseriate shaggy hairs (Gaultherieae, Niedenzu, *Epigaea, Erica, Oxydendron, Pieris, Rhododendron*). Glandular hairs of the most varied forms also occur, including glandular shaggy hairs; and lastly, peltate hairs are found (*Rhododendron, Lyonia*, and *Cassandra*), some of the latter having a glandular function. Numerous anatomical characters in the leaf-structure have been determined, and these can be employed for special diagnosis. Among these are: the varied thickness of the cuticle, a coating of wax on the cuticle, the varied structure of the walls of the epidermal cells, the formation of epidermal papillae on the lower side of the leaf (*Rhododendron*, &c.), the gelatinization of the epidermis, a many-layered epidermis (*Diplycosia, Gaultheria, Pernettya*, and *Rhododendron*), various types of leaf-structure, which are often curious in the ericoid forms, sclerenchymatous fibres in the mesophyll (*Diplycosia, Gaultheria, Pernettya*), branched spicular cells in the tissue of the leaf (*Rhododendron jasminiflorum*, Hook.) and other features, which will be discussed in the special part.

2. Structure of the Leaf. With regard to this subject the literature contains papers (Vesque, Simon), which treat of the entire Order in a general comparative manner, as well as such as are only concerned with certain tribes. In the latter connexion the investigation of the Rhodoreae by Breitfeld[1], of the Arbuteae by Niedenzu[2], and of the Ericeae by Mori and Ljungström, may be mentioned.

Even the **cuticle** shows a considerable number of structural variations. Niedenzu mentions that it varies in thickness in the Arbuteae; thus it is thin in *Arctostaphylos alpina*, but very strongly developed in *A. uva ursi*. Breitfeld reports the same variation in those Rhodoreae which he investigated. Thus nearly all species of *Rhododendron* (of the sections *Vireya, Eurhododendron*, and *Osmothamnus*) are distinguished by the possession of a strong cuticle on the upper side of the leaf; in the remaining sections of *Rhododendron*, and in *R. gracile*, Low, and *R. lepidotum*, Wall., as well as in most other Rhodoreae, the cuticle remains thin. As a rule, the cuticle is less strongly developed on the lower than on the upper side of the leaf, as is usual in other Orders. An exception to this rule is only afforded by a few species, especially among those of the genus *Cassiope*, the leaves of which are closely adpressed to the stem, the lower side being exposed to the sun and to free access of air, and exhibiting the stronger cuticle. The occurrence of cuticular ridges, which arise by folding of the cuticle and may occasionally attain a considerable height, is very common. Gruber records such cuticular ridges in all the species of *Erica* which he investigated. In the Rhodoreae they appear to be wanting, or are at any rate rare, to judge from Breitfeld's statements. Amongst the Arbuteae Niedenzu has met with them for example in *Gaultheria antipoda*, Forst., and has found them to be, on the whole, widely distributed in many species of *Arbutus* (*A. Andrachne*, L., &c.). Simon names

[1] Breitfeld investigated numerous species of the genus *Rhododendron*, as well as species of the genera *Rhodothamnus, Leiophyllum, Menziesia, Daboecia, Kalmia, Bryanthus, Loiseleuria, Phyllodoce* and *Ledum*.

[2] The material investigated by Niedenzu consisted of species of the following genera: (*a*) in the group Arbuteae: *Arbutus* and *Arctostaphylos*; (*b*) in the group Andromedeae: *Enkianthus, Pieris, Lyonia, Andromeda, Cassiope, Cassandra, Leucothoë, Agauria, Agarista, Zenobia, Oxydendron, Epigaea* and *Orphanidesia*; (*c*) in the group Gaultherieae: *Gaultheria, Diplycosia, Pernettya* and *Chiogenes*. When the Arbuteae, Andromedeae, and Gaultherieae are spoken of in the following description, these groups are to be taken as delimited by Niedenzu in the manner just indicated.

Befaria phyllireaefolia and *B. grandiflora*, as well as the genus *Grisebachia* in this connexion. In some cases a coating of wax has been observed on the cuticle (*Andromeda dealbata*, according to De Bary, and *A. polifolia*, L.). Other structural characters relate to the differentiation of the **epidermal cells** themselves. Their lateral walls may be either straight or undulated. In the simplest case, the epidermis consists of one layer, and we shall first refer to the structural peculiarities of this simple epidermis. Its cells generally have a cubical or flat tabular shape. Only rarely do they show a high rectangular, palisade-like form in transverse section, e.g. in *Arbutus Unedo*, L., and *Pernettya serpyllifolia*, DC., according to Niedenzu, and in some species of *Leucothoë* (*L. nummularia*, &c.), according to Simon. The epidermal cells also exhibit differences with regard to the thickness of their walls. Thus, according to Niedenzu, they have thin walls and wide lumina in *Arctostaphylos alpina*, *Enkianthus himalaicus*, Hook. fil. et Thoms., and *E.* (*Meistersia*) *cernuus* (Sieb. et Zucc.), thick walls and narrow lumina in some species of *Arctostaphylos*, in *Chiogenes hispidula*, Torr. et Gray, in the species of *Cassiope* and other Andromedeae. Similarly, according to Breitfeld, the epidermal cells are small and have thick walls, in the species of the section *Osmothamnus* of *Rhododendron*, also in *Leiophyllum buxifolium*, Ell., *Rhodothamnus Chamaecistus*, Reichenb., and *Kalmia angustifolia*, L., whereas in the species of the sections *Azalea*, *Tsusia*, *Rhodorastrum*, *Azaleastrum*, and *Therodendron* of the genus *Rhododendron* they are large and have delicate walls. Strong thickening of the internal cell-walls of the epidermis (i. e. those parallel to the leaf-surface) is a special peculiarity, found in *Cassandra* (*Lyonia*) *ferruginea* (Nutt.) Niedenzu and *Pieris phillyreaefolia*, DC. Simon observed reticulate thickening on the external walls in *Leucothoë pulchra*, and the same structure is found on the lateral walls of the epidermal cells in *Pyrola* (*Ramischia*) *secunda*. According to Simon, gelatinization of the internal walls of the epidermal cells is very widely distributed in the tribes Ericeae and Rhodoreae; on the other hand, Simon did not observe this feature in any of the Arbuteae, Andromedeae, and Pyroleae. Radlkofer records gelatinization of the epidermis in *Erica carnea*, *E. multiflora*, *Calluna vulgaris*, and *Arbutus Unedo*; as further examples, Simon mentions *Blaeria ericoides*, *Kalmia*, and *Befaria*, whilst Gruber quotes the species of *Erica*, investigated by him, and Vesque *Rhododendron retusum*. According to my own investigation, *Rhododendron gracile*, Low, has similar gelatinized epidermal cells, the inner portions of which penetrate deeply into the mesophyll; this species, by the way, has a simple epidermis, contrary to Breitfeld's description, the structure in question having been quite incorrectly interpreted by him in the species of *Rhododendron* mentioned, and perhaps also in other species of the section *Vireya*. The formation of papillae on the lower epidermis remains to be mentioned. According to Breitfeld and Vesque, they are found in numerous species of *Rhododendron*, in *Kalmia glauca*, Ait., and *K. latifolia*, L.; in *Kalmia glauca*, Ait., the papillae are long and hair-like, and devoid of a lumen (Fig. 110, *A*). The many-layered epidermis, of which I am now about to speak, has hitherto only been observed in the Arbuteae and Rhodoreae, and not in the Ericeae and Pyroleae. Breitfeld has given a detailed description of the many-layered epidermis of the genus *Rhododendron* and distinguishes two cases. In the first case, the cells of the individual layers (up to three in number) are essentially similar to one another in structure, e.g. in the species of the section *Eurhododendron*. In the second case, the epidermis consists of two layers and the lower layer is distinguished from the upper one by the specially large size of the cells; this is the case in most species of the section *Vireya* (with regard to *R. gracile* see above). I may add that in *R. jasminiflorum*, Hook., which belongs to the section *Vireya*, the cells of the second layer show gelatinization of their internal membranes. With regard to the group investigated by

Niedenzu, he describes the epidermis in the species of the section *Euagarista* of the genus *Agarista* as consisting of two or three layers in places only, since only a certain number of the epidermal cells undergo secondary division by means of horizontal or oblique walls into 2–3 cells. Niedenzu observed a typical many-layered epidermis in numerous species of *Gaultheria* and *Pernettya* and in *Diplycosia heterophylla*, Bl. In this case the various cell-layers of the epidermis are either of similar structure, as in *Rhododendron*, or the inner cells are distinguished by their considerable size.

The **stomata** are, as a rule, situated on the lower side only of the leaves. In the species with rolled leaves, they are without exception found only in the grooves on the lower surface. Stomata are present on both sides of the leaf in *Arctostaphylos tomentosa*, Dougl., *Epigaea repens*, L., *Pyrola minor*, L., and *Cassiope hypnoides*, Don ; they are present only on the upper side in *Cassiope lycopodioides*, Don, the leaves of which are adpressed to the stem and have palisade cells on their lower side. The stomata are never distinctly sunk below the surface, whilst in this Order in very many cases they project above the level of the epidermis. This is the case, for example, in the species of the sections *Vireya* and *Eurhododendron* of *Rhododendron*, according to Breitfeld, and invariably in those species in which the stomata are situated in grooves. An important point of difference from the Vacciniaceae lies in the fact that in the Ericaceae the stomata are, as a rule, surrounded by several neighbouring cells, which have no distinctive shape. According to Niedenzu, it is quite exceptional to find in the Ericaceae one (as in *Gaultheria Ehrenbergiana*, Klotzsch, but not in all species of *Gaultheria*) or several (*Diplycosia*) subsidiary cells, placed parallel to the pore on both sides of the pair of guard-cells.

The **mesophyll** shows bifacial structure in most cases. Centric leaf-structure has only been observed in a few species ; among these are *Erica cupressina*, according to Ljungström, in which a single layer of palisade-tissue is found beneath the whole of the epidermis, and species of *Arctostaphylos*, according to Niedenzu, in which the entire mesophyll is composed of palisade tissue. In the Rhodoreae, the varied relative thickness of the palisade and spongy tissues is of systematic value, according to Breitfeld. From amongst Niedenzu's statements we may first mention that the arms of the cells of the spongy tissue are either developed only in one plane, parallel to the leaf-surface, or on all sides (' flat-armed ' and ' spreading-armed ' spongy cells). In the forty-six species of *Gaultheria* investigated by Niedenzu, the cells of the spongy tissue are flat-armed ; in *Pernettya* cells of both shapes occur. Spongy cells with thick walls have been observed by Niedenzu in species of *Gaultheria* and *Pernettya* ; a bellows-like folding of the longitudinal walls of the palisade-tissue is found in species of *Arbutus* and some Gaultherieae. The differentiation of the mesophyll is especially characteristic in the **rolled leaves** of the species of *Erica*, the grooves of which, as may be mentioned in passing, originate secondarily on the lower side of the leaf, just as in *Empetrum*, according to Ljungström, Mori, and Gruber ; thus it comes about that the outer surfaces of the margins of the leaf, which appear to be revolute, belong to the lower and not to the upper side of the leaf. The rolled leaves of *Erica* have either one or two grooves, according to Ljungström ; in the grooves spongy tissue occurs above (internal to) the epidermis, which is provided with stomata at these points ; on all other parts of the leaf an epidermis devoid of stomata occurs, and beneath (internal to) it there is generally palisade-tissue (for details see Ljungström). The curious leaves of *Cassiope Redowskii*, Don, and other species also belong to the class of rolled leaves ; according to Niedenzu, they have the form of a pocket, open below and of lanceolate outline. The outer wall of these pocket-shaped leaves is composed of two parts, viz. that part which, ascending from the point of insertion, is adpressed to the stem and corresponds to the upper side of

the leaf, and that part which joins on to the former below, but is turned away from the axis and belongs to the morphologically lower side of the leaf; this entire outer surface has an epidermis devoid of stomata and, below that, spongy tissue (in the outer wall of the upper side of the leaf) or palisade-tissue (in the outer wall of the lower side of the leaf); the inner wall of the pocket, on the other hand, has an epidermis provided with stomata and subjacent spongy tissue. Other species of *Cassiope*, such as *C. lycopodioides*, Don, *C. Mertensiana*, Don, &c., have no such rolled leaves, but the leaves are flatly adpressed to the stem, and are characterized by the development of spongy tissue on the upper side and of palisade parenchyma on the lower side, while the stomata are limited to the upper side. Finally, the following special structures occurring in the mesophyll remain to be mentioned: sclerenchymatous fibres, running irregularly in the mesophyll (in *Diplycosia pilosa*, Bl., and *D. heterophylla*, Bl., *Pernettya brasiliensis*, Niedeuzu, *Gaultheria leucocarpa*, Bl., according to Niedenzu); slightly branched spicular cells, elongated perpendicularly to the leaf-surface, in the palisade-tissue of *Rhododendron jasminiflorum* (according to my own observations), and groups of sclerenchymatous fibres at the margin of the leaf (species of *Pernettya*, *Gaultheria*, *Leucothoë*, and *Erica*, according to Niedenzu and Ljungström).

The vascular bundles of the **veins** are mostly accompanied by mechanical tissue. The smaller veins may be either embedded or vertically transcurrent.

Oxalate of lime is excreted[1] in the form of clustered or solitary crystals.

The **trichomes** exhibit very great variety in their degree of differentiation. In order to give a suitable comparative description, I divide them into three classes, viz.: (*a*) clothing hairs (in the narrower sense, not taking into account clothing hairs of peltate shape); (*b*) glandular hairs (in the narrower sense, excluding glandular hairs of peltate shape); (*c*) peltate hairs, which will be discussed separately, their function being partly clothing, partly glandular.

The clothing hairs, taken in the sense just mentioned, are in the simplest case ordinary unicellular trichomes, either long, with thin walls, or shorter, with thick walls; both forms are widely distributed in the Order. A further type is constituted by simple uniseriate hairs. Long hairs of this type, composed of elongated cells of approximately equal length, are found in many Andromedeae. Other simple uniseriate hairs consist of a basal portion, composed of a small number of almost isodiametric cells, and of a terminal portion composed of a few elongated cells, e.g. in the genus *Arbutus*. Finally, the conical, uniseriate hairs of *Kalmia glauca*, Ait., are composed of rather numerous short cells with thick walls. The tufted hairs of the genus *Clethra* may be considered as a modification of the simple unicellular type; they consist of a variable number of simple unicellular hairs, inserted side by side in the epidermis. Breitfeld observed branched,abietiform hairs (Fig. 110, *B*) in species of *Rhododendron* (not enumerated); these trichomes form a modification of the uniseriate clothing hairs. Another type of clothing hairs may be comprised under the name of shaggy hairs (Fig. 110, *C*), which, at any rate at the base, consist of a varying number of rows of cells. They are often of considerable length, but may occasionally be short. Sometimes certain cells at the periphery of the hair have pointed ends which project as papillae; these are directed towards the tip of the hair, which thus acquires a distinctive appearance. The clothing shaggy hairs in question are recorded by Niedenzu as characteristic of the Gaultherieae, but he also observed them in *Oxydendron arboreum*, DC., *Epigaea repens*, L., and *Pieris floribunda*, Benth. et Hook. Breitfeld mentions similar shaggy hairs as

[1] It may be pointed out that according to Zimmermann (see Pflanzenzelle, 2. Heft, 1891, p. 127) crystalloids in the nuclei occur in the stem- and leaf-tissue of *Pyrola*.

occurring in species of *Rhododendron*, belonging to the sections *Azalea* (where they had already been observed by Rauter), *Tsusia*, *Rhodorastrum*, *Azaleastrum*, *Therodendron*, and especially *Eurhododendron*; Vesque records them in species of *Erica* (such as *E. ciliaris*). Related to these simple shaggy hairs, there is a series of other forms of trichome which likewise come under the heading of shaggy hairs. Firstly, we have the hairs which Niedenzu describes and figures in *Arctostaphylos tomentosa*, Dougl. These possess a short, multiseriate base, composed of almost isodiametric cells and sunk in the epidermis of the leaf; a hair-cell is attached to the end of this basal part. Other forms belonging to the same class are the broom-shaped shaggy hairs, which Breitfeld describes in *Rhododendron Falconeri*, Hook. f., *R. lanatum*, Hook. f. (Fig. 110, *D*), and *R. fulgens*, Hook. f., and the stellate shaggy hairs, which the same author mentions in *Rhododendron grande*, Wight (Fig. 110, *E*), *R. Falconeri*, Hook. f., and *R. Hodgsoni*, Hook. f., but which he inappropriately associates with the true peltate hairs of *Rhododendron*. The broom-shaped shaggy hairs of *R. Falconeri*, &c., consist of a multiserate stalk of short cells, to which is attached a bundle of uniseriate branches, directed upwards. The stellate shaggy hairs of the above-mentioned species of *Rhododendron* are a modification of the broom-shaped form; their stalk is short, and consists of a few rows of cells; the uniseriate rays point in all directions.

The second class of trichomes, distinguished above, is that of the glandular hairs, excluding those of peltate form. These also appear in the most varied shapes. In *Arbutus*, *Arctostaphylos alpina*, and *A. tomentosa*, Dougl., in *Enkianthus*, and in *Gaultheria Myrsinites*, Hook., and *G. hispida*, R. Br., the glandular hairs are of the shaggy type, i.e. they are multiseriate hairs, which vary in their degree of development, and are crowned by a glandular head composed of a few cells. In a second series of glandular hairs the head is more strongly developed than the stalk, and in this series we may include the following forms. *Lyonia ligustrina*, DC. (Fig. 110, *F*), the species of *Pieris* of the section *Eupieris* and also *Pieris mariana*, Benth. et Hook., possess glandular hairs, in which the short stalk is generally one cell, and only locally two cells, in breadth, and bears a long elliptical head, consisting of two rows of somewhat elongated cells. *Cassiope fastigiata*, Don (Fig. 110, *G*), has glandular hairs with a unicellular stalk and a head which consists of a single elongated ellipsoidal cell, or of several similar cells, arranged like a row of beads and constricted at the joints. The glandular hairs last referred to are also found in *Cassiope selaginoides*, Hook. fil. et Thoms. The glandular hairs of the species of *Pieris* belonging to the sections *Portuna* and *Phillyreoides*, have a short ellipsoidal or spherical multicellular head and a relatively long biseriate stalk (Fig. 110, *H*). The glandular hairs of *Leucothoë axillaris*, Don, and *L. Catesbaei*, Gray (Fig. 110, *J*), are, in reality, simply multiseriate shaggy hairs, composed only of short cells; their upper part, consisting of cells with thin walls and forming the elongated elliptical glandular head, is scarcely marked off from the basal portion, the cells of which have thicker walls. In the Rhodoreae Breitfeld also observed glandular hairs, which belong to our present subject; they occur in *Ledum*, *Phyllodoce*, *Bryanthus*, and in *Rhododendron lanatum*, Hook. f., and *R. campylocarpum*, Hook. f. They have a short stalk and an ellipsoidal head, which shows a network of polygonal cell-surfaces externally. In these two species of *Rhododendron*, twin glandular hairs sometimes occur, two glandular heads crowning the biseriate stalk of the hair (Fig. 110, *K*).

The peltate hairs, of which I am now about to speak, are found in the genera *Rhododendron*, *Lyonia*, and *Cassandra*. In its most typical form the peltate hair of *Rhododendron* consists of a short, multiseriate stalk and a shield made up of two areas of cells, an inner circular disc and an outer annular zone. The first of these areas presents a network of polygonal cells in surface view, whilst

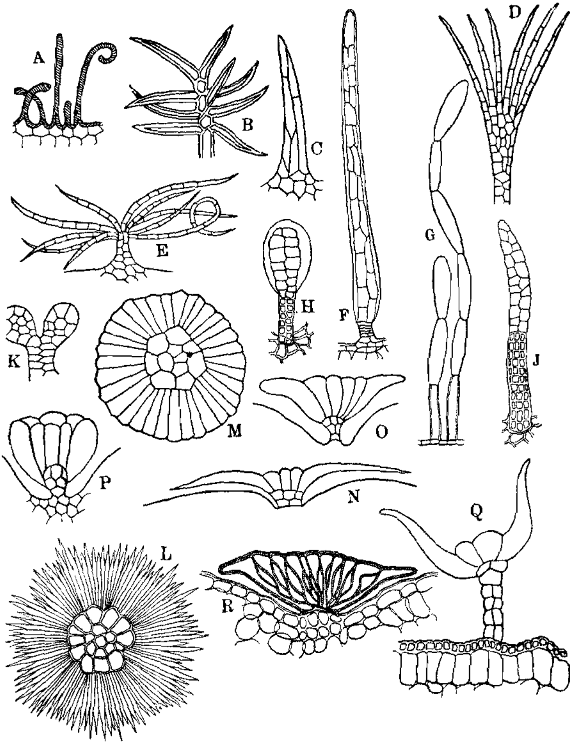

FIG. 110. Forms of trichomes, found in the Ericaceae. A, Papillae of the lower side of the leaf of *Kalmia glauca*, Ait. B, Abietiform hair, from *Rhododendron*, sp. C, Shaggy hair of *R. sinense*, Sweet. D, Broom-shaped shaggy hair of *R. lanatum*, Hook. f. E, Stellate shaggy hair of *R. grande*, Wight. F, External gland of *Lyonia ligustrina*, DC. G, External gland of *Cassiope fastigiata*, Don. H, External gland of *Pieris floribunda*, Hook. fil. J, Glandular hair of *Leucothoë Catesbaei*, Gray. K, Double glandular hair of *Rhododendron lanatum*, Hook. fil. L, Peltate hair of *R. album*, Bl. M, N, Peltate hair of *R. malayanum*, Jack. O, Peltate hair of *R. Dalhousiae*, Hook. fil. P, Bud-shaped peltate hair of *R. pendulum*, Hook. fil. Q, Cup-shaped peltate hair of *R. Anthopogon*, Don. R, Peltate gland of *R. ferrugineum*, L.—A–E, K, M–P, after Breitfeld; F–J, after Niedenzu; L and Q, after O. Bachmann; R, after De Bary.

the second consists of a simple ring of ray-cells, elongated in the direction of the radius of the shield (Fig. 110, *L, M, N*). Peltate hairs of this kind are mentioned by O. Bachmann as occurring in *Rhododendron album*, Bl., and in some cases in *R. Anthopogon*, Don, by Breitfeld in *R. caucasicum*, Pall., and *R. malayanum*,

Jack. If all the cells of the shield, both those of the central area and those of the margin, be imagined to be equally strongly elongated in the direction of the stalk, but in such a way that the marginal cells still appear as ray-cells in the surface-view of the shield, peltate hairs would be obtained, such as are mentioned by Breitfeld as occurring in *R. Dalhousiae*, Hook. f. (Fig. 110, *O*). If all the cells of the shield were elongated still more in the direction indicated, and to an equal extent, bud-shaped hairs would result, which would differ considerably from the peltate form; such are described by Breitfeld in *R. pendulum*, Hook. f. (Fig. 110, *P*). Finally, if the cells of the ray alone grow upwards in the direction of the stalk, whilst the cells of the central area are arrested in longitudinal growth, hollow cup-shaped hairs will arise, which approach nearer to the peltate form, and in which the cells of the central area form the bottom, and those of the margin form the wall of the cup; to this type belong some of the peltate hairs of *R. Anthopogon*, Don (Fig. 110, *Q*). Other peltate hairs of *Rhododendron* are partly glandular in function, as has been stated above. According to De Bary, these peltate glandular hairs belong to the category of intramural glands (Fig. 110, *R*). Their secretion is not only deposited between the cuticle and the underlying walls of the cells of the shield, but also between the longitudinal walls of these cells; these longitudinal walls are placed perpendicularly or obliquely to the surface of the shield and intercellular spaces are formed between them by their separation. *R. ferrugineum*, *R. hirsutum*, and *R. caucasicum*, for example, have glandular peltate hairs of this kind, according to De Bary. The almost spherical heads of the larger glandular hairs of *Ledum* belong to the same category, according to De Bary and Vesque. In these hairs the head consists (to make use of De Bary's words) of 9–10 cells, diverging radially from the end of the stalk. The polygonal outer walls of these cells are disposed in the periphery of the sphere and remain in lateral contact with one another without any intercellular spaces, the parts of the cuticle belonging to the different cells being firmly fused together. Towards the interior, the lateral cellulose-walls rapidly narrow down to small tubes, which meet at the top of the stalk and leave a wide space, completely filled with resinous secretion, between their walls. Finally, the peltate hairs of the genera *Cassandra* and *Lyonia* remain to be discussed. They are shortly stalked and their shield exhibits polygonal cells in surface view, as I have observed in *Cassandra calyculata*, Don, and in an undetermined species of *Lyonia*; the marginal cells of the shield are little if at all radially elongated. According to Niedenzu, peltate hairs of this kind occur[1] in two species, which were formerly included in *Lyonia*, but were transferred by him to *Cassandra*, probably on account of the occurrence of peltate hairs (viz. *C. ferruginea* (Nutt.) Niedenzu, and *C. jamaicensis* (Don) Niedenzu).

3. Structure of the Axis. The structure of the axis has hitherto only been made the subject of investigation to a small extent. With regard to the structure of the **wood** the following facts may be mentioned[2]. The vessels of the wood may be either very numerous, as in *Meisteria* or *Gaultheria*, or rela-

[1] Vesque considers the trichomes recorded by him (loc. cit., p. 230) in *Rhododendron argenteum*, but not clearly shown in his Fig. 14, to be metamorphosed peltate hairs; according to my own investigation of dried material they are trichomes of apparently glandular function, which have a short stalk, consisting of a few rows of cells and surmounted by a larger number of tubular, thin-walled cells, lying in one plane.

At this point the club-shaped or cylindrical glandular shaggy hairs, observed by Hanstein on the bud-scales of *Azalea indica*, may be mentioned. Their cells are arranged in transverse tiers made up of a few cells and the latter again in radial series, which meet in the longitudinal axis of the hair; the secretion is produced between the walls of the individual cells.

[2] The following species have been investigated: *Arbutus Andrachne*, L.; *Arctostaphylos uva ursi*, Spreng.; *Erica carnea*, L.; *Philippia abietina*, Klotzsch; *Gaultheria ferruginea*, Ch. et Schl.; *Meisteria cernua*, S. et Z.; *Menziesia ferruginea*, Smith; *Rhododendron hirsutum*, L.

tively few in number, as in *Erica*. They are scattered and do not have large lumina (maximum diameter = ·024 – ·045 mm.). Spiral thickening of the vessel-wall has been observed in *Arbutus Andrachne* and *Arctostaphylos uva ursi*; in *Rhododendron hirsutum* and *Menziesia ferruginea* only the ends of the vessels are spirally thickened. The bordered pits of the vessel-walls are usually small. They are also to be found on those portions of the wall which are in contact with parenchyma of the medullary rays. The mode of perforation of the vessels varies, but all species investigated exhibit a tendency to form scalariform perforations. In *Calluna vulgaris*, Salisb. (according to Chalon) and the species of *Erica* and *Philippia* mentioned in the second footnote on p. 486, as well as in those of *Arbutus* and *Arctostaphylos*, the perforations of the vessels are, as a rule, simple, being circular or elliptical; scalariform perforations with few bars, however, occur in smaller numbers. In the above-mentioned species of *Rhododendron*, *Menziesia*, *Gaultheria*, and *Meisteria*, the perforations are almost solely scalariform and never simple; in *Meisteria cernua* they even have many bars. In *Menziesia ferruginea*, moreover, we often find curious malformed perforations, viz.: separate small round holes on the same dividing wall of the vessel and without any regular arrangement, or circular holes placed in a ring, or circular and slit-shaped holes, combined to form one perforation, &c. The vessels of *Meisteria cernua* occasionally exhibit dividing walls of elongated elliptical form, which only bear scattered groups of small pits; it has not been determined whether these pits are perforated. The vessels with transverse walls of this type have the same diameter as those having scalariform perforations. Scalariform perforations in the vessels have also been observed in other members of the Order by various authors, viz. in *Clethra* by Schacht, and in species of *Ledum*, *Calluna*, and *Pyrola* by Tangl. The medullary rays of the wood are only uniseriate in *Rhododendron* and *Menziesia*, elsewhere they may be as much as four cells in breadth. The wood-parenchyma is usually only developed in small amount; it is present in greater quantity in the investigated species of *Philippia* and *Meisteria*. With regard to the structure of the wood-prosenchyma, the following facts may be mentioned. The investigated species of *Arctostaphylos* and *Arbutus* have wood-prosenchyma with simple pits accompanying that with bordered pits and spiral thickening. The former kind seems to be wanting in the other species, or at any rate only to occur sparsely.

The structure of the **cortex** has been still less investigated than the structure of the wood. Its anatomy is known in detail only in *Erica arborea*, L., *Clethra arborea*, Ait., and *Rhododendron Nuttallii*, Booth, which Möller has examined. In a considerable number of species periderm-formation is known to be internal, the cork originating immediately to the interior of the bundles of primary bast-fibres, or when these are absent, at the outer limit of the soft bast. Vesque mentions cork-formation in this position in the genera *Leucothoë*, *Kalmia*, *Clethra*, *Azalea*, *Ledum*, *Zenobia*, *Macleania*, *Lyonia*, *Psammisia*, *Arctostaphylos*, *Andromeda*, and *Rhododendron*. The remaining particulars regarding the structure of the cortex are taken from Möller's statements. The cork-cells are large in *Rhododendron*, and are moderately flattened and uniformly thickened; in *Erica* and *Clethra* they have delicate walls or are sclerosed on one side only. The primary cortex contains no collenchyma, but has numerous large clustered crystals. Möller met with primary bast-fibres in *Rhododendron* only, not in *Clethra* or *Erica*. In the secondary bast of *Erica arborea* and *Rhododendron Nuttallii* bast-fibres are present, and are arranged in simple tangential rows in the first-named species. The secondary bast of *Clethra arborea* only contains sclerenchymatous rod-cells. Möller observed solitary crystals in one case only, viz. in the bast of *Clethra*. According to Simon, the bast-fibres in this Order possess bordered pits; Simon, however, as it appears, only examined the hard bast in the veins of the leaf.

The structure of the **pith** has been examined by Gris in a large number of genera. Quoting from the results of this investigation, it may be mentioned that the majority of the genera (*Arbutus*, *Arctostaphylos*, *Azalea*, *Befaria*, *Calluna*, *Cladothamnus*, *Cassandra*, *Erica*, *Gaultheria*, *Kalmia*, *Ledum*, *Leiophyllum*, *Menziesia*, *Phyllodoce*, and *Rhododendron*) have a homogeneous pith. Besides the active cells, others containing crystals occasionally take part in the formation of this tissue in a varied degree. Thus they are represented in small numbers in *Arbutus*, *Azalea*, *Phyllodoce*, and *Rhododendron*, whilst in *Ledum* and *Cladothamnus* the crystal-cells which have wide lumina and thinner walls form a network between the smaller active cells; in *Calluna* the internal portion of the pith consists of crystal-cells of similar structure. Other genera, viz. *Clethra*, *Elliotia*, *Leucothoë*, *Lyonia*, *Oxydendron*, *Pernettya*, and *Pieris*, are distinguished from those named above by possessing a heterogeneous pith, which again shows various special modes of differentiation. In *Pernettya*, the ground-mass of the pith consists of active cells with small lumina and thick walls, among which are scattered groups of larger cells which have thinner walls and are empty or contain crystals; *Elliotia*, *Lyonia*, and *Pieris* show similar characters. In *Clethra* the peripheral portion of the pith is formed by active cells with small lumina and thick walls, the central portion principally by empty, thin-walled cells, traversed by a network of the active cells. The same division of the pith into a peripheral portion, composed of active cells with thick walls and small lumina, and a central part, composed of empty cells with thinner walls and larger lumina, is also shown by *Zenobia floribunda*, *Oxydendron arboreum*, and *Leucothoë axillaris*; in these the central part contains specially large cells with clustered crystals.

In connexion with the discussion of the axis it may be mentioned that, according to Van Tieghem, the **roots** in a few cases have ridge-like thickenings of the cell-wall in the layers situated outside the endodermis; they are especially well seen in *Clethra arborea*, occurring in the first place on the tangential and radial walls and extending from these on to the horizontal walls, on which they meet in the form of a star. In *Arbutus Andrachne* this 'appareil de soutien' is developed differently; here the whole surface of the radial and tangential walls is thickened. Finally the presence of endotrophic mycorrhiza in the root-system of our native members of the Order (according to Frank) may be referred to.

Literature: Chalon, Tig. lign. dicotyl., Mém. i, 1867, p. 49.—Hanstein, Harz- u. Schleimabs., Bot. Zeit. 1868, pp. 729 et seq. and Tab. xii.—Rauter, Trichombild., Denkschr. Wiener Akad. 1871, pp. 17, 18 and Tab. v.—Gris, Moëlle, Nouv. Arch. Mus. d'hist. nat., t. vi, 1870, pp. 242–50 and pl. 13.—Radlkofer, Monogr. v. *Serjania*, 1875, p. 104.—Vesque, Anat. d. l'éc., Ann. sc. nat., sér. 6, t. ii, 1875.—Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 64, 65 and 360.—De Bary, Vergl. Anat., 1877.—Mori, Strutt. delle foglie delle E., Nuov. Giorn. bot., vol. ix, 1877, pp. 153, 154.—Möller, Rindenanat., 1882, pp. 203–5.—Gruber, Anat. u. Entw. d. Bl. v. *Empetrum* etc., Diss., Königsberg, 1882, 38 pp.—Ljungström, Blad. bygn. inom fam. E., Acta Lund., vol. xix, 1882–3, n. vi, 47 pp. and 2 tab.—Mori, Strutt. delle foglie delle E., Nuov. Giorn. bot., vol. xv, 1883, pp. 278–81 and tav. vii–viii.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. i, 1885, pp. 225–40 and pl. 11.—Solereder, Holzstr., 1885, pp. 161, 162.—O. Bachmann, Schildh., Flora 1886, separate copy, pp. 18, 19 and Tab. viii, ix.—Kerner, Pflanzenleben i, 1887, p. 277 et seq.—Breitfeld, Anat. Bau d. Rhododendroideae etc., Engler, Bot. Jahrb., Bd. ix, 1888, pp. 319–79 and Tab. v, vi.—Van Tieghem, Résean sous-endodermique, etc., Bull. Soc. bot. de France 1888, p. 273 and Ann. sc. nat., sér. 7, t. viii, 1888, p. 226 et seq.—Douliot, in Ann. sc. nat., sér. 7, t. x, 1889, p. 373.—Drude, in Natürl. Pflanzenfam., iv. Teil, Abt. 1, 1889, pp. 2, 4 and 16 et seq.—Lalanne, Feuilles persist., Act. Soc. Linn. de Bordeaux, sér. 5, t. iv, 1890, p. 43 et seq. and Tab. ii.—Niedenzu, Anat. Bau d. Arbutoideae etc., Engler, Bot. Jahrb., Bd. xi, 1890, pp. 134 and 177 et seq. and Tab. iv–vi.—Simon, Vergl. Anat. d. Epacrid. u. E., Engler, Bot. Jahrb., Bd. xiii, 1891, pp. 15–46 and Tab. ii.—Macfarlane, Min. struct. of hybrids, Transact. R. Soc. Edinburgh 1892, pp. 237 and 251 et seq. and pl. vii.—[Bastin, Struct. of *Epigaea repens*, Americ. Journ. of Pharm. 1895, pp. 231–6.]—Wittlin, Kalkoxalattasch., Bot. Centralbl. 1896, iii.—[Poulsen, in Vidensk. Meddelels. fra naturh. For. i Kjöbenhavn 1897.—Holm, *Pyrola aphylla*, Bot. Gazette 1898, p. 247 et seq.—Rommel, Anat. Unters. über die Gr. d. Piroleae u. Clethraceae, Diss., Heidelberg, 1898, 53 pp. and 1 Tab.]

MONOTROPEAE.

This small Order, consisting only of nine genera with few species, is, in the first place, characterized by the absence of chlorophyll Its members, as far as is known, are all saprophytes. Chatin described parasitism in young plants of *Hypopitys multiflora* and even figured haustoria; but in spite of repeated attempts, none of the more recent observers have been successful in confirming Chatin's statement.

In correspondence with the saprophytic mode of life, the structure of axis and leaf is very simple. The axis contains a ring of isolated vascular bundles, which show no secondary thickening. The leaves have a homogeneous mesophyll, composed of isodiametric parenchymatous cells. Stomata are only met with exceptionally (and not in all the Monotropeae) on the axis or on the lower side of the leaf. Oxalate of lime is absent. The hairy covering consists of simple, unicellular trichomes and of glandular hairs, which vary in structure.

The anatomy of the following species has been described in detail by Chatin: *Pterospora andromedea*, Nutt., *Monotropa uniflora*, L., *Hypopitys lanuginosa*, Nutt., *H. multiflora*, Scop., *Schweinitzia odorata*, Ell., and *Sarcodes sanguinea*, Torr. We owe a more recent, thorough investigation of *Monotropa* to Drude and Kamienski, and there is a similar work on *Sarcodes* by Oliver.

The **axis** in all cases contains a ring of vascular bundles which do not grow in thickness. In a certain number of species the vascular bundles are directly embedded in the slightly differentiated, parenchymatous ground-tissue of the stem, as in *Schweinitzia odorata* and *Sarcodes sanguinea*. In other species (*Pterospora andromedea, Monotropa uniflora, Hypopitys lanuginosa*) the bundles of the stem are embedded in a rather broad, mechanical, strengthening ring, which separates the pith from the external cortex. The cells of this strengthening ring are lignified, shortly prosenchymatous or parenchymatous, and frequently exhibit slit-like pits on their walls. The structure of the axis of *Hypopitys multiflora* resembles that of the species last mentioned, but here the strengthening-ring is locally traversed by strips of ground-tissue, resembling medullary rays. According to Caspary and Kamienski, the tracheae in the xylem of the bundles of *Monotropa* are only cells and not true vessels. The tracheal elements of the wood in the other genera are described as annular, spiral, and pitted vessels by different authors, but it remains to be determined whether perforations really occur. The bast-groups of the bundles have only been closely examined in *Sarcodes* and *Monotropa*; they contain sieve-tubes with distinct sieve-plates in the first-mentioned genus only (Oliver, Kamienski).

In the **leaf** the epidermal cells have straight lateral walls in all cases, and the mesophyll is composed of nearly isodiametric cells. Stomata have been met with in small numbers, and only on the lower side of the leaf in *Pterospora andromedea, Monotropa uniflora*, and *Hypopitys lanuginosa* (on the other hand, they have not been found in the remaining three species, enumerated above); in *Pterospora* they also occur on the stem.

There are no statements concerning the occurrence of **oxalate of lime**. On the other hand, special tannin-containing cells with rather wide lumina have been demonstrated (Kamienski) in the ground-tissue and vascular system of the stem of *Monotropa*.

The **hairs** in this Order do not belong to any uniform type. In *Pterospora andromedea* the following forms have been observed: simple, unicellular

hairs, which may become glandular and in that case acquire a slight knob-like swelling of their tip; glandular shaggy hairs with a multiseriate stalk and a head, which is either composed of polyhedral cells or of a single layer of cells, elongated like a palisade in the direction of the stalk; finally, glandular hairs with unicellular or uniseriate stalks and with heads having the same structure as in the glandular shaggy hairs. Shaggy hairs of varying shape and consisting of several rows of cells, in which it is usually impossible to recognize a sharp distinction between head and stalk, occur in *Sarcodes*; in *Hypopitys* simple unicellular hairs and occasional unicellular bottle-shaped glandnlar hairs are found.

NOTE.—The roots of *Monotropa* and *Sarcodes* are provided with an ectotrophic mycorrhiza. The exogenous origin of the lateral roots in *Sarcodes* and *Pterospora* (but not in *Monotropa*), according to Oliver, is an abnormal occurrence and therefore noteworthy.

Literature: Chatin, Anat. comp., Pl. parasit., Paris, 1856-65, pp. 244-96 and pl. xlix-lv.—Caspary, in Monatsber. Berliner Akad. 1862, p. 467.—Drude, Biol. v. *Monotropa Hypopitys*, Göttingen, 1873. —Kamienski, Org. vég. du *Monotropa Hypopitys*, Mém. Soc. nat. d. sc. nat. de Cherbourg, t. xxiv, 1882, pp. 5-40 and pl. i-iii (here also the older literature).—Drude, in Natürl. Pflanzenfam., iv. Teil, Abt. i, 1889, pp. 4, 5.—Oliver, *Sarcodes*, Ann. of bot., vol. iv, 1890, pp. 303-26, pl. xvii-xxi.

EPACRIDEAE.

1. REVIEW OF THE ANATOMICAL FEATURES. A series of anatomical characters which are common to the members of this Order may be mentioned in the first place. The hairy covering is very scanty, and only consists of simple unicellular hairs or, in extremely rare cases, of uniseriate hairs. Glandular hairs are entirely wanting, and so are special internal secretory receptacles, including mucilaginous epidermal cells in the leaf. The epidermal cells of the leaf are in nearly all cases elongated in the direction of its long axis and have undulated lateral walls. The stomata, which are never depressed below the surface, lack special subsidiary cells; their pores are placed parallel to one another and almost always lie in the direction of the midrib of the leaf, only exceptionally (*Lysinema*) transversely to it. According to Simon, the sclerenchymatous fibres which accompany the vascular systems of the veins are characterized in all the species by the bordered pitting of their walls (Fig. 111, *C*). In the structure of the axis, the vessels, which have small lumina and perforations exhibiting a tendency to become scalariform, the narrow medullary rays, the wood-prosenchyma with bordered pits, and perhaps also the internal formation of cork appear to be of importance for the anatomical diagnosis of the Order. The following special characters in the leaf-structure are of value for anatomical diagnosis: the thickness of the cuticle; the varied structure of the walls of the epidermal cells, e.g. occurrence of thickening-ridges on the outer wall, &c.; the formation of papillae on the epidermis of the lower side; the distribution of the stomata on both sides of the leaf, or their restriction to the upper or lower epidermis; special arrangements for the enclosure of the stomata (Fig. 111, *A–B*); the varied construction of the leaf (mesophyll); the diverse structure of the veins, viz. embedded veins and such as are vertically transcurrent below or both above and below.

2. STRUCTURE OF THE LEAF. There is a comprehensive work by Simon[1]

[1] Simon investigated the following genera: (*a*) in the tribe Stypheleae: *Styphelea*, *Coleanthera*, *Astroloma*, *Conostephium*, *Melichrus*, *Cyathodes*, *Pentachondra*, *Trochocarpa*, *Brachyloma*, *Needhamia*, *Lissanthe*, *Leucopogon*, *Monotoca* and *Oligarrhena*; (*b*) in the tribe Epacreae: *Epacris*, *Lysinema*, *Archeria*, *Prionotis*, *Lebetanthus*, *Cosmelia*, *Sprengelia* (*Ponceletia*), *Andersonia*, *Richea*, *Dracophyllum*.

on the leaf-structure of this Order, and in the following account I give an abstract of his observations.

The **integumental system** of the Epacrideae, as in the Ericaceae, affords a large number of anatomical characters, some of which are of value even for the diagnosis of the Order. Most important among these is the shape of the epidermal cells. They are rarely flat and tabular, but usually show a quadratic shape in the transverse section of the leaf, or their height may even exceed their breadth. In surface view the epidermal cells, especially those of the upper side, are usually considerably elongated in the direction of the midrib of the leaf, in correspondence with the generally elliptical shape of the latter; occasionally they are more or less distinctly arranged in longitudinal rows. An exception is afforded by the isodiametric epidermal cells of *Dracophyllum muscoides*, Hook. fil., while *Cyathodes acerosa*, R. Br. and *Conostephium pendulum*, Benth. are distinguished by specially marked elongation of these cells. The lateral walls of the epidermal cells are undulated in nearly all cases, excepting only some species of *Coleanthera*, *Dracophyllum*, *Epacris*, *Leucopogon*, and *Styphelia*. The cuticle is strongly developed in almost all the species; only a few of them (e.g. *Epacris paludosa*, R. Br., *Leucopogon australis*, R. Br., and *Lysinema lasianthum*, R. Br.) which grow in damp places have a weak cuticle. The latter is especially thick, for example, in *Richea scoparia*, Hook. f., and *Cyathodes parvifolia*, R. Br.; in these species it attains a thickness of 11–12 μ. In some cases the function of the cuticle is supplemented by a deposit of wax. The walls of the epidermal cells of *Pentachondra pumila*, R. Br. and of those of the lower side of the leaf of *Styphelia elegans*, Sond. have a peculiar structure. The cells show swollen thickenings on their lateral walls, projecting convexly into the interior of the cells in such a way that they appear like stone-cells in a superficial section. In *Styphelia elegans* the internal walls of the lower epidermal cells, as well as the portions of the lateral walls abutting on them, are so strongly thickened that the lumen of the epidermal cell is of conical shape with the wider opening towards the exterior. In a few cases Ambronn noticed a further structural feature in the wall of the epidermal cells, viz. the strengthening of the outer walls by means of thickening-ridges on their internal surface. Simon found this character in *Epacris petrophila*, Hook. fil. and *Leucopogon australis*, R. Br. on the upper side of the leaf alone, in *Lysinema conspicuum*, R. Br. only on the lower side, in *Epacris obtusifolia*, Sm., *Lysinema lasianthum*, R. Br. and *Dracophyllum rosmarinifolium*, Forst. on both sides. Papillose differentiation of the lower epidermis occurs in species of *Leucopogon* and *Styphelia*, if I understand Simon rightly. The latter did not observe gelatinization of the epidermal cells in this Order; probably there can be no question of this feature having been overlooked, since the same author has demonstrated it in a number of Ericaceae. On the whole, it appears that the integumental tissue in the Epacrideae does not require water-storage to such an extent as in many Ericaceae. A typical many-layered epidermis has been observed in *Dracophyllum Traversii*, Hook. f., by Areschoug; Simon, if I understand him rightly, describes an epidermis, consisting locally of many layers, as occurring in *Cyathodes acerosa*, R. Br. and *Lissanthe strigosa*, R. Br.

The small **stomata** are, as a rule, confined to the lower side of the leaf. In the species with grooved leaves they occur only in the grooves; this is the case in *Stenanthera pinifolia*, R. Br., *Leucopogon tetragonus*, Sond., and others, in which only two grooves are present, as well as in *Conostephium pendulum*, Benth., *Lissanthe strigosa*, R. Br., and *Melichrus rostratus*, R. Br., which have numerous grooves. The stomata occur on both sides of the leaf in *Andersonia*, in the majority of the species of *Dracophyllum* and in other species of the tribe Epacreae, i.e. for the most part in plants with leaves which are closely adpressed to the stem. In the leaves of *Leucopogon cucullatus*, R. Br., *L. cymbiformis*,

A. Cunn., &c., which are likewise closely adpressed to the stem, the stomata however occur on the upper side of the leaf alone. It may be noted that the pores of the stomata are parallel to the long axis of the leaves, which are generally elongated and narrow. The species of the genus *Lysinema* form an exception, for here the pores are placed transversely to the long axis. Special subsidiary cells accompanying the stomata are not present in the Epacrideae. The stomata are usually situated on a level with the epidermis; but occasionally they are elevated above its surface, as in *Cyathodes empetrifolia*, Hook. f., *Melichrus rotatus*, R. Br., and *Lissanthe strigosa*, R. Br. Simon did not observe depressed stomata in any member of the Order. In a number of cases, however, he observed protective structures in the stomata (Fig. 111, *A–B*) situated internal to the pore, and interfering with the interchange with the atmosphere. Since the guard-cells are mostly smaller than the neighbouring epidermal cells and are situated on a level with the outermost part of the latter, a kind of shaft is found above the actual air-chamber; this is bounded by the lower portions of the vertical walls which belong to the cells adjoining the stomata, and are in contact with the pair of guard-cells; hence this shaft connects the pore with the air-chamber. The exchange of gases between the pore and the air-chamber is impeded in some cases by the outgrowth of club-shaped thickenings from the vertical walls which limit the shaft (Fig. 111, *B*), these thickenings coming to be in close contact with one another (species of *Andersonia*, *Lysinema*, *Needhamia*, *Oligarrhena*, *Ponceletia*); in other cases the vertical walls bounding the shaft become uniformly and strongly thickened (Fig. 111, *A*) in such a way that the passage from the air-chamber to the guard-cells can only be recognized as a fine slit, the direction of which coincides with that of the pore between the guard-cells (species of *Epacris*, *Archeria*, and *Oligarrhena*). Still more complicated arrangements for enclosing the stomata are shown by *Dracophyllum latifolium*, Cunn., regarding which reference must be made to Simon's original treatise.

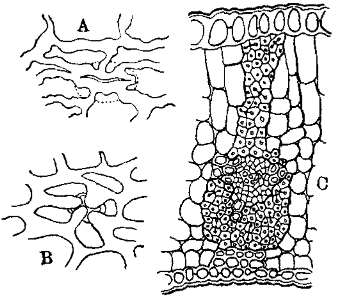

FIG. 111. A, B. Surface-view of a stoma of *Archeria eriocarpa*, Hook. fil. (A) and *Ponceletia sprengelioides*, R. Br. (B) with the accompanying neighbouring cells, seen from the inside. C, Section of a vein of the leaf of *Richea dracophylla*, R. Br.—After Simon.

The **leaf-structure** is bifacial in most cases. The small leaves of *Lysinema* and *Andersonia*, in which palisade-parenchyma is found on both sides, have centric structure. In some species of *Dracophyllum* palisade-tissue is absent, the assimilating cells being of isodiametric shape. In many species those walls of the cells of the spongy tissue which border on the air-chambers are considerably thickened.

According to Simon, the structure of the thicker **veins** of the leaf is of great systematic value. Three cases may be distinguished: (1) embedded veins provided with a sheath of sclerenchyma, in *Epacris*, *Lysinema*, *Archeria*, *Prionotis*, *Lebetanthus*, *Cosmelia*, *Sprengelia* (together with *Ponceletia*), and *Andersonia*[1]

[1] In species of *Andersonia* and *Ponceletia*, veins which are vertically transcurrent above by means of sclerenchyma are to be found as an exceptional case in the sheathing portion of the leaf.

(i. e. in most Epacreae), further, amongst the Styphelieae, in *Needhamia*, *Oligarrhena*, and *Trochocarpa*, and finally, as an exception in *Dracophyllum muscoides*, Hook. f.; (2) veins which are vertically transcurrent below by means of sclerenchyma, in nearly all Styphelieae and in *Sphenotoma* pro parte; (3) veins which are vertically transcurrent above and below by means of sclerenchyma, forming I-shaped girders, in *Richea* (with *Cystanthe* and *Pilites*) and *Dracophyllum* (with *Sphenotoma* pro parte), and also in the thickest veins of species of *Leucopogon*.

The sclerenchymatous fibres which form the mechanical sheath of the vascular bundles of the leaf, have narrow lumina and thick walls of exceedingly curious structure, since they are covered with typical bordered pits in all the members of the Order (see Fig. 111, *C*). Simon also demonstrated bordered pitting of the bast-fibres in the branches of some species. The physiological function of these sclerenchymatous fibres with bordered pits is however not the transmission of water, as might be concluded from the structure of their walls. They are, in so far as fresh material has been investigated, living cells, and many facts point to their taking part in the conduction of plastic substances.

Special **secretory receptacles** are wanting in this Order, just as in the Ericaceae and the other allied Orders. In Simon's work oxalate of lime is merely stated to occur occasionally in the form of solitary crystals accompanying the sclerenchyma of the veins. I have also met with it in this form in the cortex of the branches.

The **hairy covering** is very uniform, and thus differs from that of the Ericaceae. Glandular hairs are entirely absent. The hairs which occur are mostly simple and unicellular, having either thick walls and narrow lumina or thin walls and wide lumina. Uniseriate hairs are rare.

FIG. 112. Modified scalariform perforation of *Epacris heteronema*, Labill.—Original.

3. STRUCTURE OF THE AXIS. The structure of the axis has hitherto been little investigated. I have examined the **wood** in *Styphelia laeta*, R. Br., *Leucopogon denudatus*, Sieb., *Andersonia caerulea*, R. Br., *Epacris microphylla*, R. Br., and *E. heteronema*, Labill., and mentioned the following facts in my 'Holzstruktur.' A transverse section of the xylem-mass shows more or less numerous scattered vessels with a small lumen (maximum diameter = ·03 mm.) and 1–2-seriate medullary rays, the cells of which are elongated in the vertical direction. The vessel-wall has bordered pits even where it is in contact with parenchyma of the medullary rays. The perforations of the vessels are, for the most part, simple in *Styphelia*, *Leucopogon*, and *Andersonia*; in the other cases they are scalariform with few or many bars. In both species of *Epacris* the ordinary scalariform perforations (with 4–20 bars) are accompanied by others of peculiar structure (Fig. 112), which are closely related to the scalariform type; the species in question, however, have no simple perforations. Spiral thickening is found at the ends of the vessels of both species of *Epacris*. The wood-parenchyma is little developed. The wood-prosenchyma probably bears bordered pits in all cases (Simon); in *Epacris microphylla* it is provided with spiral bands as well.

Regarding the structure of the **cortex**, scarcely any statements are to be found in the literature. A casual examination of *Styphelia laeta* showed that in very young branches an almost continuous ring of bast-fibres occurs in the pericycle, and that formation of cork commences very early and immediately internal to the bast-fibres. This cork is extremely peculiar and may be recommended for developmental investigation. Its cells have no distinct radial arrangement; a distinct cork-cambium is not present,

and it almost appears as though the cells of the cork originated from the outer cells of the soft bast. The secondary bast contains groups of sclerenchymatous fibres in the older portions of the cortex ; these fibres differ from the bast-fibres of the pericycle in the appearance of their transverse section and in the structure of their wall ; solitary crystals appear in their neighbourhood.

Literature : Areschoug. Bladets anat., Minnesskrift, Lund, 1878.—Ambronn, in Pringsheim Jahrb., Bd. xiv, 1884, p. 105 et seq.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. i, 1885, p. 244.—Solereder, Holzstr., 1885, p. 163.—Drude, in Natürl. Pflanzenfam., iv. Teil, Abt. 1, 1889, p. 68.—Simon, Vergl. Anat. d. E. etc., Engler, Bot. Jahrb., Bd. xiii, pp. 15–46 and Tab. ii.

DIAPENSIACEAE.

This small Order, which is very closely related to the Ericaceae, has been anatomically investigated chiefly by Grevel[1]. It should be specially noticed that the glandular hairs, occurring so widely in the Ericaceae, are absent, and that clothing hairs are only developed in *Pyxidanthera* in the form of conical unicellular trichomes with very thick walls.

The following facts may be pointed out regarding the structure of the **leaf**. The mesophyll is either bifacial or (species of *Shortia* and *Galax*) consists of uniform cells, which are isodiametric or roughly so. The epidermal cells have undulated lateral walls, and, especially on the upper side, a strongly thickened outer wall, frequently traversed by pits. *Shortia tibetica*, Franch. is characterized by papillose differentiation of the epidermal cells on the lower side of the leaf, while *Diapensia lapponica*, L. is distinguished by the presence of a considerable swelling of the thick cuticle over the middle of each epidermal cell. The stomata occur on both sides of the leaf (*Pyxidanthera*, *Diapensia*, *Shortia*, *Schizocodon*, *Galax*) or on the lower side only (*Diapensia*, *Shortia*). They are not surrounded by any special subsidiary cells (at any rate, in *Diapensia lapponica*, L., and *Galax aphylla*, L., according to my own investigation). The vascular system of the petiole shows various types of differentiation. Oxalate of lime is usually excreted in the form of clustered crystals, more rarely of solitary crystals (*Galax*). Chlorophyll is found in the epidermis of the leaf in species of *Diapensia* and *Galax*. Internal glands are absent.

In the structure of the **wood** it is important that primary medullary rays are only met with immediately above the nodes and that secondary rays are wanting. The vessels have small lumina ; in *Diapensia lapponica* the perforations are mostly simple, rarely scalariform, with few bars. The wood-prosenchyma either has bordered pits (*Diapensia*, *Pyxidanthera*), or in part simple pits (*Shortia*, *Schizocodon*, *Galax*). The medullary sheath is sclerenchymatous, and is, for the most part, composed of parenchymatous cells, elongated in a vertical direction. The pith may have thick or delicate walls. The phloem has a swollen collenchymatous appearance. Superficial development of cork has been shown to occur in *Galax*, and pericyclic development in *Diapensia* and *Pyxidanthera* (cork-cells, thickened in the form of a U in the latter).

LENNOACEAE.

This Order, like the last, is a small one, indigenous to South California and Mexico. It only consists of the three genera *Pholisma*, *Ammobroma*, and *Lennoa*, which are root-parasites, devoid of chlorophyll. They are parasitic on

[1] Anat. Untersuch. über d. Familie d. Diapensiaceae, Bot. Centralbl. 1897, i, n. 9–13, p. 257 et seq. and Taf. ii ; this investigation comprises the structure of the axis and leaf in the genera *Pyxidanthera*, *Diapensia*, *Shortia*, *Schizocodon*, *Galax*.—See also Vesque, Ann. sc. nat., sér. 7, t. i, 1885, p. 245.

roots of *Eriodictyon*, *Clematis*, and unidentified species of the genus *Prosopis*, and they develop a shoot from a few inches to a metre in height; this often lies buried up to the floral region in the sand of the desert. The little we know concerning the anatomy of these forms, and especially of the genera *Ammobroma* and *Lennoa*, is due to the work of Solms-Laubach[1], on whose statements our entire knowledge of this interesting Order practically depends.

A transverse section of the **stem** of *Lennoa* or of *Ammobroma* shows a ring of large isolated vascular bundles accompanied by smaller cortical bundles. The pith (situated internally to the ring of vascular bundles) and the primary cortex are of identical structure; they consist of rounded-polygonal cells and contain numerous starch-grains. In *Ammobroma* the xylem of the bundles of the ring is (except for the spiral and annular vessels, present at the margin of the pith) exclusively composed of pitted and reticulate vessels with rather wide, almost circular lumina; the division-walls in these vessels have simple, round perforations; in *Lennoa* isolated elongated and rather thin-walled cells occur between the vessels of the xylem. The phloem contains sieve-tubes. The epidermis of the stem, which possesses stomata, bears glandular hairs, in which the stalk is unicellular or uniseriate, whilst the head is represented by an enlarged terminal cell, rich in protoplasm, and shaped like a knob or bladder. Glandular hairs of the same type, it may be added, are also found on the leaves of *Lennoa* and on the tips of the calyx-lobes of *Ammobroma*; on these latter, the uniseriate stalk occasionally forks into two arms, which are directed upwards or placed horizontally, each of them bearing a glandular head.

Regarding the structure of the **scale-leaves** covering the stem, it is sufficient to mention that they possess stomata on both sides or only on the lower side (*Lennoa* sp., Schaffner n. 452), and that the stomata (in *Lennoa*, sp.) are surrounded by several ordinary epidermal cells.

In the upper portion of the stem of *Ammobroma*, where it enlarges to form the floral receptacle, there are essential deviations from the structure described above. There is no differentiation into pith and cortex. A transverse section shows innumerable and irregularly scattered vascular bundles. The parenchymatous ground-tissue is formed by polygonal cells, which are considerably thickened at the corners after the manner of collenchymatous cells, but exhibit a small intercellular space in the middle of each of these thickenings.

No details concerning the internal or external connexion of the parasites in question with their host-plants are known. The few facts that have come to light are contained in Solms-Laubach's treatise, which is cited in the footnote, but they must be passed over here.

PLUMBAGINEAE.

This Order with its eight genera has been well investigated anatomically. All the species possess one anatomical character in common, namely, epidermal glands (Fig. 113) exhibiting the same structural plan. The essential and secreting portion of these glands, whether they appear as a component part of the epidermis or actually project as hairs, whether they consist of many or few cells, and whether they excrete carbonate of lime or mucilage, in all cases consists of cells elongated like a palisade and placed perpendicularly to the organ on which the glands occur. In addition to these highly characteristic glands, which will be described in detail below, we also find long-stalked glandular shaggy hairs, in which the structure of the head approaches that of the

[1] Solms-Laubach, Abh. der naturf. Gesellsch. zu Halle, 1869, pp. 119 to 178, and 3 Plates.—See also Drude, in Natürl. Pflanzenfam., iv. Teil, Abt. 1, 1889, p. 12.

epidermal glands just referred to; simple unicellular hairs also occur. The type of stoma varies. The wood contains vessels with simple perforations; the wood-prosenchyma, when present, has simple pits. In the structure of the cortex the superficial origin of the cork and the occurrence of a ring or isolated groups of sclerenchymatous fibres in the pericycle may be mentioned. Oxalate of lime is not common, but has been observed in the form of clustered and solitary crystals. In many species cells, filled with plumbagin, occur in the stem and root, and are sometimes distinctly differentiated like secretory cells. The following special anatomical characters appear in certain cases: medullary and cortical vascular bundles in the stem, the former in species of *Statice* (concentric with central phloem) and *Acantholimon* (collateral and inversely orientated), the latter in species of *Aegialitis*, *Armeria*, *Limoniastrum* and *Statice*; the occurrence of anomalous structure in the stem (groups of soft bast in the wood) in *Acantholimon* and *Aegialitis*; groups of sclerenchymatous fibres in the pith and in the primary cortex in species of *Statice*; inequalities of the surface of the stem, caused by cellular prominences of the primary cortical tissue, which enclose sclerenchymatous cells, in species of *Ceratostigma* and *Vogelia*; spicular cells in the mesophyll of species of *Statice*, *Aegialitis* and *Limoniastrum*.

After this general review I will next proceed to a detailed account of the **glands**. These may be divided into two types, according to their structure. The first type is formed by those glands which are usually described in the literature as chalk-glands or as Mettenius- or Licopoli-glands, after the names of the botanists who first observed them. They are to be found on the lamina of the leaf or on the branch in all members of the Order (including *Aegialitis*, contrary to Wilson's statement). These structures are not of the nature of hairs; they only consist of small groups of a few epidermal cells, and in most cases excrete carbonate of lime on their external surface. The second type may be termed mucilage-glands[1], this being the name given to them by Wilson, who observed them in all the eight genera, but not in all the species, employed in his investigation; they are confined to the upper surface of the leaf-sheaths. The mucilage-glands consist of a larger number of cells than the chalk-glands, and excrete a mucilaginous substance; in rare cases they are only composed of groups of epidermal cells shaped like a palisade, thus resembling the chalk-glands; in most cases they are true trichomes.

The chalk-glands (Fig. 113, *A–C*) consist essentially of almost hemispherical groups of eight cells shaped like a palisade (not four, as was incorrectly stated by Mettenius and recently repeated by Maury); according to De Bary, these eight cells originate from an epidermal cell which is rounded-quadrate in surface view. This cell becomes divided into four by two walls at right angles to one another and perpendicular to the surface; each of the cells thus formed is then divided once more by a vertical wall into two cells, one of which is very narrow and forms the inner corner while the other is peripheral. The walls of these glandular cells are extremely thin, with the exception of those which separate the internal surface of the gland from the neighbouring tissue; these latter are suberized. The contents of the glandular cells consist of dense, finely granular protoplasm. In those cases in which the structure has been thoroughly investigated, the eight-celled group of glandular cells is cut off from the internal tissue by a double cap, each layer of which is composed of four 'subsidiary' cells, so arranged that they appear as semilunar appendages of the glandular cells when examined in surface-view and at a sufficiently low focus. The cells of the upper cap (which directly encloses the group of glandular cells) have

[1] In the following description the glands of the Plumbagineae are definitely described as chalk- or mucilage-glands, although it has been proved that the excretion of these respective substances is *not constant in all cases*.

suberized walls and occasionally (Fig. 113, *A–B*) reach to the level of the glandular cells, so that they appear in a surface-view of the gland as a four-celled ring, surrounding the circular group of glandular cells; neither of these two characters applies to the 'subsidiary' cells of the second cap. The function of the chalk-glands is the excretion of water. The water is not conducted to the gland by means of tracheides, but by the ordinary cells of the tissue lying nearest to it; consequently these cells are sometimes grouped

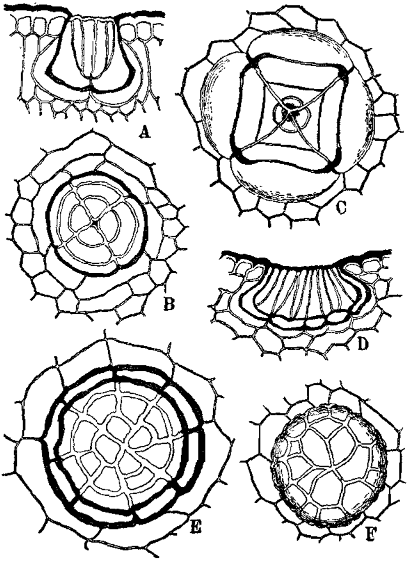

FIG. 113. A–C, Structure of the ordinary glands of the Plumbagineae: Glands from the surface of the leaf of *Aegialitis annulata*, R. Br. A, Transverse section; B, Surface-view from outside; C, from within. D–F, Mucilage-gland on the leaf-sheath of *Aegialitis annulata*, R. Br. D, Transverse section; E, Surface-view from outside; F, from inside.

radially about the gland. The emission of superfluous salts of lime is generally [1] combined with the excretion of water by the glands. The extrusion of these substances in the secreted water probably takes place in the form of bicarbonate of lime, which then becomes deposited over the gland as the neutral carbonate, owing to the action of atmospheric agencies. Deposits of lime, which are visible to the naked eye as small knobs or scales, originate in this way; occasion-

[1] Sometimes mucilage is excreted, as in mucilage-glands, e. g. on young leaves of *Statice fruticans*, Webb (Wilson).

ally as a secondary phenomenon they may cover the entire surface of an organ (e. g. a leaf) owing to the action of rain-water. The amount of lime excreted is naturally related to the nature of the soil of the habitat, and consequently varies considerably in some species, whilst in others a certain degree of constancy in this respect has been demonstrated.

According to Volkens, the lime forms a uniform covering on the leaves of certain species of *Acantholimon*, *Goniolimon*, *Limoniastrum* and *Statice*; it only forms scattered calcareous scales on the leaves of certain species of *Ceratostigma*, *Plumbago*, *Statice* and *Vogelia*; while a few species of *Plumbago*, the majority of the species of *Statice*, and almost all species of *Armeria* are quite devoid of calcareous excretions.

The physiological significance of these chalky excretions consists in a protection against excessive transpiration and hence in a regulation and diminution of the loss of water through the activity of the glands. As a prevention against too great activity of the latter, additional arrangements are, according to Volkens, found in those species which grow in very dry localities. Thus, as a first example, the chalk-glands in nearly all species of *Acantholimon*, in *Limoniastrum* and in a few species of *Statice*, e. g. *S. speciosa*, L., are depressed below the level of the epidermal surface after the manner of depressed stomata. The same result is attained when the epidermal cells which adjoin the gland become more or less elevated above the surface of the organ, thus giving rise to the structures known to systematists as tubercles; the gland lies in a depression at the tip of these tubercles. Such tubercles occur in *Statice spathulata*, Desf., *S. scabra*, Thunb., &c. The elevation of the adjacent cells and the depression of the gland have an additional object; they facilitate the retention of the excreted mass of lime. The protrusion of the epidermal cells adjoining the glands, in the form of simple hairs, seen in *Statice elata*, *S. latifolia*, Sm., and *S. Sareptana*, Beck., acts in the same way. A similar result is attained by the peculiar shape of the small pits, situated above the glands in *Limoniastrum monopetalum*, Boiss.; these pits resemble a four-pronged anchor, a shape which is naturally shared by the chalk-masses which occupy them.

The glands of the second form found in the Order, the mucilage-glands, have already been shortly described above, where they were divided into two series, viz. those which are developed as hairs, and those which are not so. The mucilage-glands of the latter type are only found in *Aegialitis*; in their structure they approach nearest to the chalk-glands. Each mucilage-gland consists: (1) of a group of thin-walled epidermal cells, elongated like a palisade, their lower portions penetrating deeply into the tissue of the leaf-sheath; and (2) of a double layer of subsidiary cells, of which those adjacent to the palisade-cells have suberized cell-walls. Seen from the surface, the gland has a circular outline; for further details see Fig. 113, *D–F*. In the remaining seven genera the mucilage-glands are hair-like structures. In this case the gland generally appears as a low prominence, which is flattened above and has a circular outline. Its upper portion consists of a rather large number of palisade-like cells, which have thin walls and are occasionally divided more or less regularly by transverse walls; its lower portion, often marked off as a very short stalk, is composed of a layer of low cells [1], which are polygonal in surface-view and are suberized. These glands are really simply mucilage-glands of the *Aegialitis*-type raised above the level of the epidermis, and as an exception they may occur on conical emergences (*Statice Sareptana*, Beck. and *S. caspia*, Willd., according to Wilson). The mucilaginous secretion of these glands varies greatly in amount; thus in *Statice rosea*, Sm., and *S.*

[1] Wilson's Fig. 21 on Pl. xi, loc. cit. is not correct; the cell-layer figured above the palisade-layer is not present.

fruticans, Webb., it is considerable, while in *Acantholimon* mucilage is most commonly not excreted at all.

In the long-stalked glandular shaggy **hairs**, which are present in the floral region (e. g. on the calyx of *Plumbago capensis*), the structure of the terminal portion (head) approaches that of the chalk- and mucilage-glands very closely. Thus the innermost portion of the head consists of a parenchymatous mass of tissue surrounded by a layer of suberized cells, having polygonal outlines in surface-view, while externally there is a layer of palisade-like epidermal cells. The stalk of the glandular shaggy hairs is multiseriate and contains a fibro-vascular strand. In addition to the glandular shaggy hairs, simple unicellular hairs are rather common in the Order.

With regard to the structure of the **leaf**, the following facts may be mentioned. The epidermal cells, as a rule, have wide lumina, and usually a thick cuticle, which is occasionally striated. Their lateral walls may be straight or undulated. The stomata occur on both sides of the leaf, and usually in equal abundance. They are, for the most part, irregularly orientated, but in the species of *Statice* and *Acantholimon* with narrow leaves they lie with their pores parallel to the longitudinal axis of the latter. They are either on a level with the epidermis or are depressed. Some species (*Armeria plantaginea* and *Acantholimon venustum*, primarily those species of both genera which have grass-like leaves) have stomata with subsidiary cells, which are placed parallel to the pore; other species (*Statice speciosa*) have stomata with three subsidiary cells; in others again (*St. imbricata*) the stomata are surrounded by ordinary epidermal cells which are irregularly arranged. Development of the stomata according to the Cruciferous type, therefore, certainly does not take place in all cases, although Strasburger describes it as being quite general in the Order. The mesophyll possesses varied structure, as one is led to expect from the nature of the leaves, which are in some cases flat, acicular in others. In *Plumbago europaea*, for example, the mesophyll is a homogeneous tissue, composed of rounded cells; in *P. Larpentae* and *Statice elata* it is bifacial; in the flat leaves of *Limoniastrum monopetalum* and the acicular leaves of *L. Guyonianum*, Dur. it has centric structure. The vascular system of the veins is sometimes accompanied by sclerenchyma, e. g. in *Statice elata* or *Aegialitis annulata*, R. Br., in which the smaller veins are vertically transcurrent on both sides by means of a layer of very slightly sclerosed palisade-cells with slit-like pits; in other cases there is no sclerenchyma, as in *Plumbago Larpentae*. Sclerenchymatous cells occur in the mesophyll of *Statice cylindrifolia* in the form of fibrous elements, which are situated in the palisade-tissue; they appear in the form of branched spicular cells (internal hairs) in *Aegialitis annulata* and *Limoniastrum Guyonianum*, Dur. (but not in *L. articulatum*, Mch., contrary to the statements of De Bary and Woronin).

The structure of the **petiole**, and especially the number of vascular bundles traversing it, varies greatly (for details, see Maury).

With regard to the structure of the **axis**, it may first be specially mentioned that the vessels have simple perforations. Where wood-prosenchyma occurs, it has simple pits. The structure of the wood in the herbaceous species shows considerable diversity, the chief part of it being either composed of unlignified tissue or of wood-fibres, while the xylem-portions of the vascular bundles are either separated from one another by rather broad medullary rays, or the rays are absent, and so on (for details, see Maury). The following features in the structure of the cortex are especially noteworthy: the subepidermal development of the cork (*Aegialitis annulata*, *Limoniastrum monopetalum*) and the presence of a ring or groups of sclerenchymatous fibres in the pericycle. According to Maury, the groups of sclerenchymatous fibres in the pith and primary cortex, which were mentioned above, are

present in all the species of *Statice*[1] examined by him; according to the same authority cellular prominences of the cortical parenchyma, enclosing sclerenchyma, are to be found in *Ceratostigma abyssinicum*, *Vogelia africana* and *V. indica*; cortical vascular bundles[2] occur in *Aegialitis annulata* and *Limoniastrum monopetalum* according to Maury, in *Armeria splendens* according to J. E. Weiss, in *Armeria plantaginea* and *Statice latifolia* according to Schwendener; the medullary bundles[2], which mostly have concentric structure with central soft bast, occur according to Maury in *Statice Limonium* (concentric), according to Russow in *S. Sareptana*, Beck. and *Goniolmon eximium*, Boiss., according to Möbius in *Statice caspia*, Willd. and *S. serotina*, Reichenb. (=*S. Limonium*), according to Scott and Brebner in *Acantholimon glumaceum*, Scop., and according to my own observation in *Statice latifolia*, Sm. (simply collateral and inversely orientated)[3].

Typical **anomalous structural features of the axis** are found in the genera *Acantholimon* and *Aegialitis*. In *Acantholimon* the appearance of successive rings of growth is combined with the occurrence of the medullary vascular bundles previously mentioned. It has not yet been determined whether the first secondary ring of bundles arises in the pericycle or in the bast-portion of the original vascular ring. Krüger first demonstrated the occurrence of this anomaly in an undetermined species of *Acantholimon*; then it was investigated by me in a species identical with or very closely related to *A. libanoticum*, Boiss., and finally by Scott and Brebner in *A. glumaceum*, Boiss. The anomaly which I have recently met with in the genus *Aegialitis* and especially in *A. annulata*, R. Br., is similar to that of *Acantholimon* as far as its appearance in transverse section is concerned, but it has quite a different course of development as far as could be determined from an examination of herbarium-material. In transverse section, young branches of the plant show a normal ring of vascular bundles, the bast-groups of which are separated from the primary cortex by bands of sclerenchymatous cells. The layer of cells situated immediately on the outside of the sclerenchymatous bands subsequently becomes a meristem, producing a xylem-ring internally, in which lamellae, composed of soft bast, are enclosed, while no phloem is formed externally. The original ring of vascular bundles is thus closely surrounded by the secondary xylem-ring, so that both together form a single mass of wood, in which the original soft bast and the interxylary groups of soft bast belonging to the anomalous increment of wood appear to be embedded as cell-groups of similar structure. It could not be determined with certainty in what way the groups of soft bast of the secondary anomalous xylem-ring are formed, i. e. whether they are produced on the outer or inner side of the meristem; probably, however, the latter is the case. The anomaly just described in *Aegialitis* approaches most closely to that of *Stylidium adnatum* (see Stylidiaceae), among known anomalies.

Note.—For the root-structure see Maury. Here mention need only be made of the fact that the fibres in the wood of the root in *Statice Kaufmanniana*, similar to the tracheids of *Juniperus*, are characterized by peg-like or beam-like projections, which arise from the thick wall and project into the cavity of the fibre or stretch transversely across it.

Literature: Mettenius, Filices Hort. bot. Lips., 1856, p. 10.—Oliver, Struct. of the stem of Pl. &c., Transact. Linn. Soc. vol. xxii, part 4, 1859, pp. 289 to 294 and tab. 50, 51.—Licopoli, in Ann. dell' Accad. degli asp. naturalisti di Napoli, 1866.—Strasburger, in Pringsheim Jahrb., Bd. v, 1866–7,

[1] According to Möbius they are also present in *Goniolimon eximium*, Boiss. = *Statice eximium*, Schrenk.

[2] The following statements refer in part at any rate to the axes of inflorescences.

[3] According to Scott and Brebner the medullary vascular bundles of *Acantholimon glumaceum* arise relatively late from a secondary meristem, and the latter occasionally appears in a curious position—external to the primary vessels of the normal ring of bundles.

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PRIMULACEAE.

1. Review of the Anatomical Features. The following features are specially important: the lack of a special type of stomatal apparatus, the development of a characteristic endodermis with Caspary's dots on its radial walls around the vascular bundles, and the occurrence of glandular hairs with a unicellular or multicellular head, which in the latter case is divided by vertical walls only. In addition to the glandular hairs, simple, uniseriate and multicellular branched trichomes (in *Androsace*) take part in forming the hairy covering of the Primulaceae. The perforations of the vessels are simple in the few cases observed (*Androsace, Lysimachia*); the development of cork (rhizome of *Primula*) is internal. Oxalate of lime has not been described as occurring in any member of the Order. The following types of secretory organs are present: secretory cells with red contents (*Anagallis, Centunculus, Lysimachia*); closed (schizogenous) secretory cavities with the same secretion, which often has a sphaero-crystalline structure (*Lysimachia, Coris, Samolus,* and *Androsace*); these are connected by transitions with ordinary intercellular spaces having similar contents (*Lysimachia*); finally, there are ordinary intercellular spaces, provided with a mucilaginous lining (*Primula*). Deviations from normal structure are found in the stem and rhizome of certain species of *Primula,* which may be shortly described as Auriculas, and in *Hottonia.* A transverse section of the rhizome or stem in the Auriculas (Fig. 115) shows several rings of vascular bundles (' steles ' of Van Tieghem), often devoid of a pith, in place of the normal ring of bundles. The ' steles ' are arranged in a circle or are quite irregularly placed, and the stem-structure of the Auriculas is thus polystelic. In addition to this, a network of vascular bundles is developed secondarily in the pericycle of these steles; this is connected with the fibro-vascular system of the adventitious roots and is termed ' réseau radicifère ' by Van Tieghem. The same ' réseau radicifère ' also occurs in those species of *Primula* which are collectively termed *Officinales* by Van Tieghem. Their stem or rhizome shows normal structure, i. e. a single ring of bundles, and is thus ' monostelic.' The water-plant *Hottonia* has a vascular system of concentric structure in its stem with central xylem and secondarily formed pith, arising from wood-parenchyma.

2. Structure of the Leaf. This is sufficiently well known in the sixteen

[1] This plant, a sterile portion of the branch of which was investigated by Woronin, is not *Statice monopetala*, L. = *Limoniastrum articulatum*, Mch. It was determined as such by Woronin on anatomical grounds on account of the branched sclerenchymatous cells of the leaf, which were erroneously described for *Statice monopetala* by De Bary (Vergleich. Anat.).

genera[1] examined by Kamienski. It is essentially the same throughout, and only varies in so far as the nature and consistency of the leaves are different. The **epidermis** is, in most cases, characterized by undulated lateral walls; the high epidermal cells of *Samolus littoralis*, however, are provided with straight lateral walls. It has already been indicated above, that the **stomata** have no specialized adjacent cells, but are surrounded by three or more ordinary epidermal cells. In *Primula* stomata are found on both surfaces of the leaf, and are even occasionally (*P. Auricula*) more numerous on the upper side. The aquatic *Hottonia* develops few or no stomata on its submerged leaves. Water-pores, from one to three in number, are frequently (*Soldanella Clusii, Primula Auricula, P. acaulis*, and other species, *Hottonia*) present on the leaf-teeth; in *P. sinensis* there is an epithema beneath them, to which a vascular bundle extends (De Bary). The leaf-structure is bifacial.

Three kinds of **secretory receptacles** are found in the Order: secretory cells, schizogenous secretory cavities provided with an epithelium, and ordinary intercellular spaces which are not closed and are filled with a secretion. The secretory cells, which have reddish-brown contents, have been observed in the roots of *Lysimachia Nummularia, L. punctata*, and *L. vulgaris* (De Bary), in the leaf of *Anagallis coerulea* and *Centunculus minimus* and in the pith and cortex of *Anagallis repens*, DC. and *A. latifolia*, L. (Kamienski). The numerous red dots in the leaves of *Anagallis coerulea* and *Centunculus minimus* are caused by these cells. The closed secretory cavities are confined to the genera *Lysimachia* incl. *Naumburgia* and *Lubinia*, *Coris* and *Samolus*[2], according to Bokorny; to these I can add *Androsace* with *A. lactea*, L. on the basis of a casual observation of my own; Kamienski is wrong in describing groups of secretory cells as occurring in this species. According to Bokorny, the schizogenous secretory cavities are generally not constant for the genus, at any rate not as regards their occurrence in the leaf; thus they are absent in the leaf of *Lysimachia ciliata*, L., *L. evalvis*, Wall., &c. Their contents resemble those in the secretory cavities of the allied Order Myrsineae, and are usually formed by a bright-red sphaerocrystalline body, which is slightly soluble in alcohol, but readily soluble in ether; these contents cause the reddish-brown or brown, transparent or opaque, dotting of the leaves. The schizogenous origin of the secretory cavities has, so far, only been ascertained

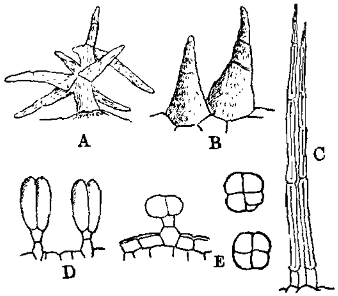

FIG. 114. Hairy covering of the Primulaceae: A, *Androsace multiscapa*; B, *A. elongata*; C, *A. arachnoidea*; D, *Cyclamen persicum*; E, *Lysimachia Nummularia*.—After Kamienski.

[1] These are: *Primula, Androsace, Dionysia, Cortusa, Dodecatheon, Cyclamen, Soldanella, Lysimachia* (incl. *Naumburgia* and *Lubinia*), *Glaux, Asterolinum, Trientalis, Coris, Anagallis, Centunculus, Hottonia* and *Samolus*.

[2] Bokorny examined the leaves of *Hottonia, Androsace, Douglasia, Dionysia, Cortusa, Soldanella, Dodecatheon, Cyclamen, Trientalis, Asterolinum, Glaux, Anagallis* and *Centunculus* with negative results. A renewed investigation of these genera, as well as of all the Primulaceae, with regard to the occurrence and differentiation of the secretory receptacles in the various organs is desirable.

in *Lysimachia*. All transitions from the closed secretory cavities just mentioned to ordinary intercellular spaces, filled with the same secretion, are found in species of *Lysimachia*. The latter, for example, are described by De Bary as occurring in the stem and root of *Lysimachia Ephemerum*, and (accompanying closed secretory cavities) also in the leaf. Lazniewski has recently described similar structures, namely intercellular spaces with a mucilaginous lining, in the leaf of a number of Primulas (in *P. Auricula*, *P. pubescens*, *P. rhaetica*, &c., but not in *P. officinalis*, *P. elatior*, &c.).

According to Kamienski, the **hairy covering** consists of clothing and capitate hairs. The former are mostly simple and uniseriate, but exhibit various forms. Thus *Androsace elongata* has short conical trichomes of two or three cells (Fig. 114, *B*), *A. maxima* has long uniseriate hairs, composed of numerous cells with wide lumina, whilst in other species of *Androsace*, the cells of the uniseriate hairs have very thick walls and narrow lumina, and may be few (*A. sarmentosa*) or many (*A. arachnoidea*, Fig. 114, *C*, *A. Chamaejasme*, *A. cylindrica* and *A. villosa*) in number. In many species of *Androsace* (*A. septentrionalis*, *A. multiscapa*, Fig. 114, *A*, *A. armeniaca*, *A. lactea* and *A. ciliata*) multicellular branched hairs occur, in which the degree of branching varies. It has already been stated in the general diagnosis that the head of the capitate hairs is either unicellular or divided by vertical walls only. Apart from the number of cells in the head, the capitate hairs differ in the shape of the latter and in the varied length of the uniseriate stalk, which may be short and bicellular or longer and composed of more numerous cells. The capitate hairs in question are, as a rule, glandular hairs, the head producing a resinous secretion below the cuticle; it is remarkable that this is also the case in the water-plant *Hottonia*. The well-known bloom which is found, for example, in *Primula Auricula* and *P. farinosa*, is the product of the secretion of these capitate hairs, and, according to De Bary, consists of crystalline particles which are readily soluble in cold alcohol (therefore not wax). The glandular hairs in question have been observed by Kamienski in all the genera mentioned above submitted to examination by him. The head of these glands is in most cases unicellular, as in *Primula*. A bicellular head is mentioned by Kamienski as occurring in *Cyclamen* (Fig. 114, *D*[1]), *Anagallis coerulea*, *Lysimachia vulgaris*, *Trientalis europaea* and *Hottonia*; a usually quadricellular head in *Lysimachia Nummularia* (Fig. 114, *E*), *Asterolinum stellatum* and *Centunculus minimus*; in *Glaux maritimus* and *Samolus* there are heads which are composed of still more numerous cells. The glandular hairs generally stand freely on the surface of the organs; in *Samolus littoralis* they are deeply sunk in the epidermis.

3. Structure of the Stem and Rhizome. All the genera investigated by Kamienski, with the exception of *Hottonia* and one group of species of *Primula*, to which I shall return below, have normal stem-structure, i. e. a ring of vascular bundles surrounding a central pith, and enclosed by an endodermis and the primary cortical tissue. The **vascular bundles** forming the ring show various features. In some members of the Order they are firmly connected with one another and grow in thickness by means of a cambium, e. g. in the perennial forms: *Primula sinensis*, *Androsace*, *Cortusa*, *Cyclamen europaeum*, *Soldanella*, *Coris*, *Lysimachia vulgaris*, &c.; in other cases the cambium is wanting, e. g. in most annual Primulaceae. The vascular bundles are often isolated and arranged in a circle in the transverse section of the stem, e. g. in *Primula mistassinica* and some species of *Androsace*. *Glaux* and *Trientalis* are transitional forms, inasmuch as the xylem-groups of the bundles are distinct, whereas the bast-groups are in

[1] A peculiar hairy covering has been shown by Hildebrand to occur on the tubers of certain species of *Cyclamen*; this is composed of the capitate hairs described above, tufted hairs (with a single stalk-cell and a varying number of ray-cells) and intermediate forms between these two types.

continuity. An endodermis was found by Kamienski in all the species investigated by him; it is readily recognized by the characteristic Caspary's dots on the radial walls. In exceptional cases the endodermal cells show very considerable thickening of their walls and a corresponding reduction of their lumen, e. g. in *Soldanella alpina* and *S. montana*. The endodermis is to be found in the root and leaf as well as in the stem. Internal to the endodermis, in the pericycle, a sclerenchymatous ring frequently occurs, e. g. in *Lysimachia vulgaris, Trientalis europaea*, and others. This ring, or rather the tendency to form such a ring, is regarded by Westermaier as a general anatomical character of the Order. In those cases in which it is wanting, its absence is easily explained, according to Westermaier, on physiological grounds, the stems in question having little need of rigidity (for details see loc. cit.). In other Primulaceae, viz. in certain species of the genus *Primula*, which will be referred to again below, a periderm is developed beneath the endodermis of the stem, and causes the latter and the primary cortex to be thrown off. In other Primulas again, namely in those of the group Officinales and in the Auriculas (sensû Van Tieghem), a system of vascular bundles is formed in the pericycle of the root-stock; this system is in direct connexion with the adventitious roots, and surrounds the system of leaf-trace bundles in the form of a complicated network (' réseau radicifère ' of Van Tieghem). With regard to the perforations of the vessels it is only known that they are simple in *Androsace* and *Lysimachia*. Medullary groups of sclerenchyma are characteristic of certain Primulas, *Cortusa Matthioli, Soldanella montana, S. alpina* and *Samolus littoralis*, R. Br. Similar groups of sclerenchyma also occur in the cortex in certain Primulas and in *Samolus littoralis*. A further consequence of the mode of life in damp localities is the presence of large intercellular spaces in the pith and primary cortex in a number of members of the Order, such as species of *Lysimachia* (especially *L. thyrsiflora*, L.); the halophytic species, *Glaux maritima*, also has large air-passages in its cortical tissue, similar to those of *L. thyrsiflora*. The schizogenous air-passages are largest in the water-plant *Hottonia*, in which they are arranged in several circles in the transverse section of the stem and are only separated by single rows of cells.

The fibro-vascular system of the stem of the water-plant *Hottonia* is anomalous. On superficial examination it seems to consist of a ring of bundles surrounding medullary tissue, as in the normal Primulaceae, except that intercellular spaces appear in place of some of the primary groups of vessels and that the secondary thickening by means of the cambial ring is slight. Closer examination, however, shows that the tissue appearing as a pith is not ground-tissue, but wood-parenchyma resembling a medulla, in the centre of which the first vessels were developed (H. Schenck).

The peculiar anomalous stem-structure of the Auriculas has already been briefly referred to above in the review of the anatomical features. It was first described by Vaupell in *Primula Auricula* and later by Kamienski, who discovered the same anomalous structure in certain other Primulas; quite recently it has again been dealt with by Van Tieghem and Douliot. These authors investigated more than 100 species of the genus *Primula*, and showed that the anomaly found in *Auricula* occurs in a considerable number of cases; and they made use of this anomalous structural feature in conjunction with other characters for a classificatory subdivision of the genus *Primula*. Neglecting a few exceptions, this classification can be brought into agreement with Duby's system in De Candolle's Prodromus.

In one group of Primulas, which, according to Van Tieghem, coincides with the genus *Primula*, Tournef., the structure of the stem (rhizome) is normal. Only a single ring of vascular bundles, a ' **stele**,' is found in the stem; the latter therefore has monostelic structure. The species exhibiting this type of structure are separated by Van Tieghem into further groups, according to their anatomical

features. Thus one series of species (Sinenses and Cortusoides of Van Tieghem) shows strong secondary thickening in the wood and bast of the stem, while another series (Officinales of Van Tieghem) has only slight growth in thickness. In the first two sub-groups the outer cortex is thrown off owing to cork-formation beneath the endodermis; in the Officinales a 'réseau radicifère,' which has already been referred to, appears beneath the endodermis. Features of less importance, and only of value for distinguishing species, are: groups of stone-cells in the pith (*Primula elatior*, *P. carpathica*, *P. cortusoides*), complete sclerosis of the pith (*P. septemloba*), groups of stone-cells in the cortex (*P. heucheraefolia*), branched groups of stone-cells in the cortex (*P. malvacea*), &c. (Cf. the synopsis in Ann. sc. nat., Sér. 7, T. III, p. 292.)

A second group of Primulas which Van Tieghem places together under the generic name *Auricula*, Tournef., differs essentially from the first group in the anomalous structure of the stem. At a distance of a variable number of

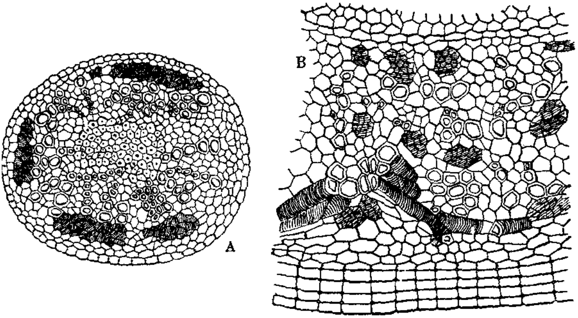

FIG. 115. A, Stele from the stem of *Primula* (*Auricula*) *glutinosa* in transverse section, formed by 4-5 vascular bundles and provided with a pith of thick-walled fibrous cells. B, Portion of the gamostelic bundle-ring of *Primula* (*Auricula*) *japonica*; on the outside is the cortical network of bundles. The soft bast is shaded in both figures.—After Van Tieghem and Douliot.

internodes above the cotyledons, there is still a single ring of vascular bundles to be seen in a transverse section. Still higher up, however, this ring appears to have split by repeated forking into several bundle-rings, 'steles,' which either do or do not possess a pith. They vary in their number and in their arrangement in a transverse section (Fig. 115, *A*). The stem of the Auriculas has numerous steles; it is polystelic. In the group of Primulas in question, the wood and bast of the stem show either no growth in thickness or only a slight amount. The outer cortex is not thrown off, and a 'réseau radicifère' is formed in the pericycle, as in the Officinales. Amongst the Auriculas only one species, *P. reptans*, forms an exception as regards the polystelic character just mentioned; it shows a stem-structure similar to that of *Hottonia*, as it possesses only one 'stele' and little pith.

The number and arrangement of the steles vary in the polystelic species. Thus there are only 2-3 steles in *Primula minutissima*, *P. glutinosa*, &c., 3-5 steles disposed in a circle in *P. angustifolia*, *P. capitellata*, &c., 8 similarly placed steles in *P. minima*, *P. Muretiana*, &c., 12 in *P. carniolica*, 20 in *P. Delavayi*. In other species the steles do not appear arranged in a circle, but irregularly scattered in the transverse section; in this case, however, a series of larger steles generally forms a ring.

The following species belong to this type: *P. pedemontana* and *P. doanensis* with 12 steles, *P. spectabilis* with 20 steles, *P. ursi*, *P. latifolia* and *P. commutata* with about 40–50 steles, *P. hirsuta* with as many as 70 or 80 steles. The steles are mostly small and round, when they are numerous (*P. Delavayi*, *P. ursi*, &c.); when they are few in number, they may likewise be small, as in *P. Allionii*, *P. angustifolia*, &c., though they are generally large and either rounded (*P. algida*, &c.) or elongated-elliptic (*P. farinosa*, &c.). The structure of the steles is as follows. The parenchymatous tissue forms zones of cells round each stele; these cells are also arranged in radial rows and are separated by small quadrangular intercellular spaces in a transverse section of the stem. The innermost of these zones is differentiated as an endodermis and shows Caspary's dots on the radial walls of the cells. The endodermis is followed internally by a pericycle of one or two layers of cells. The vascular system consists of 4–8 groups of soft bast, which are occasionally united with one another to form a ring, and has a corresponding number of groups of xylem, which are situated opposite and internal to the phloem-groups, and likewise occasionally coalesce with one another. In the interior of the stele a pith is generally wanting (*P. ursi*, *P. latifolia*, &c.); more rarely it is present. When present its cells sometimes have thin walls (*P. Balbisii*, *P. Maximowiczii*), but more frequently they are thickened and lignified (*P. spectabilis*, *P. Clusiana*, *P. glutinosa*, &c.). In those cases in which the pith of the stele is not sclerotic, groups of sclerenchyma are sometimes found in the pericycle, but only on the side which is directed towards the centre of the stem (*P. minima*, &c.); in other species scattered groups of sclerenchyma occur throughout the ground-tissue of the stem between the steles (*P. pubescens*, *P. Muretiana*, &c.). The last-mentioned groups of sclerenchymatous cells sometimes become secondarily surrounded by an annular zone of periderm (*P. pubescens*). Concerning the course of the steles it may be pointed out that they do not run parallel to one another, but anastomose in a reticulate manner. When the meshes of the network are elongated and the strands narrow, the steles are mostly isolated in a transverse section. One can then follow Van Tieghem in speaking of a 'dialystelic' structure of the stem (*P. ursi*, *P. marginata*, &c.). On the other hand, if the meshes are short and the strands of the network broad, the steles in a transverse section of the stem frequently appear arched, or even under certain circumstances fused with one another to form a single ring, which is only slightly interrupted; this structure may be described as 'gamostelic' (*P. japonica*, Fig. 115, *B*, *P. purpurea*, *P. sonchifolia*, &c.). (Cf. the synopsis of the species of *Auricula*, in Ann. sc. nat., Sér. 7, T. III, p. 305.)

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MYRSINEAE.

1. Review of the Anatomical Features. The anatomical features which are characteristic of this Order are as follows: the prevalence of simple perforations in the vessels, the simple pitting of the wood-prosenchyma, which is sometimes septate, the occurrence of bordered pits on the vessel-wall even where it is in contact with parenchyma, the lack of a special type of stoma, and the frequent occurrence of shortly stalked glandular hairs with a flatly spherical or peltate head, which is divided by vertical walls only (Fig. 116); especially in the Theophrasteae, these glandular hairs are deeply embedded in the tissue of the leaf and are then visible even to the naked eye as depressed dots. The members of the tribes Maeseae and Eumyrsineae contain schizogenous secretory cavities in the leaf, which give rise to transparent or opaque dots and lines; the corresponding secretory structures in the axis are developed as canals. The Theophrasteae lack secretory cavities, but are distinguished anatomically by the occurrence of sclerenchymatous fibres beneath the epidermis on both sides of the leaf; the differences in the mode of arrangement of these sclerenchymatous fibres enable one to distinguish the four genera belonging to this tribe. In addition to the glandular hairs, peltate trichomes of analogous structure (but not glandular) occur in the Order; further, simple uniseriate and peculiar branched trichomes are found, the latter in *Jacquinia armillaris*, Jacq. (Fig. 116, *C*). Besides the secretory cavities, resin-cells are sometimes present (pith of *Maesa* and leaf of species of *Cybianthus*) and, according to Höhnel, 'proteid-containing marginal glands and fused secretory sacs' (leaf of *Ardisia crenata*). Oxalate of lime appears in the form of clustered and solitary crystals. Other special features, which can be employed in detailed diagnosis, are the following: gelatinization of the epidermis of the leaf, development of hypoderm in the leaf, structure of the pericycle (isolated groups of bast-fibres, or a composite and continuous ring of sclerenchyma), &c.

2. Structure of the Leaf. The special features exhibited by the tissues of the leaf have been sufficiently investigated, but our knowledge of the general characters of the leaf-structure is essentially confined to what Vesque has published as the result of general comparative investigations. The leaf-structure is generally bifacial. The lateral walls of the **epidermal cells** are straight or undulated. Striation of the cuticle has been observed. In *Oncostemon* and *Myrsine capitellata* the cells of the epidermis have very large lumina. A hypoderm of one or few layers is developed in certain species of *Clavija* (*C. nobilis*, *C.* '*ornata*,' *C. Riedeliana*, *C. Rodekiana*, *C. umbrosa*) and *Jacquinia* (*J. armillaris* and *J. ruscifolia*), according to Vesque, in *Aegiceras majus*, Gaertn., according to Schimper, and in *Clavija caloneura*, Mart., according to my own observation; gelatinization of the epidermis of the leaf occurs in *Wallenia laurifolia*, Sw., *Cybianthus detergens*, Mart., *C. myrianthos*, Miq., *C. obovatus*, Mart. and *C. penduliflorus*, Mart., *Conomorpha laxiflora*, A. DC., *C. macrophylla*, Mart., and *C. nemoralis*, Mart. et Miq., *Ardisia latipes*, Mart., all according to Bokorny, and in *Parathesis crenulata*, Hook. f., according to my own observation. The **stomata** are only found on the under side, and are surrounded by three or more neighbouring cells. The vascular bundles of the **veins** have a sclerenchymatous sheath in certain species only. **Oxalate of lime** is usually deposited in the form of ordinary solitary and clustered crystals; small prismatic or acicular crystals of oxalate of lime have been met with in the epidermis of the leaf of *Deherainia smaragdina* and *Jacquinia ruscifolia*.

The schizogenous **secretory cavities** in the leaf, which are characteristic of the Maeseae and Eumyrsineae, have much greater systematic value than the majority of the features so far referred to. They have been demonstrated by Bokorny in the genera *Myrsine*, *Wallenia*, *Cybianthus* (with *Weigeltia*), *Embelia*

(with *Choripetalum*), *Conomorpha*, *Ardisia* (with *Badula*, *Climacandra*, and *Stylogyne*), *Pimelandra* and *Hymenandra*, by Radlkofer in *Maesa* [1], by Pax and Van Tieghem in *Aegiceras*, and by a casual observation of my own in *Grammadenia* (*G. parasitica*, Griseb., Eggers n. 634, San Domingo) and *Parathesis* (*P. crenulata*, Hook. f., Pringle n. 3101, Mexico). The contents of the secretory cavities either have a distinctly radiate crystalline structure or are homogeneous and vitreous, and consist of large fragments, or they are minutely granular. In some cases they are soluble in alcohol and ether; in other cases, however, they dissolve slowly only in these reagents, but readily in a solution of caustic potash. The colour of the contents varies from pale yellow to deep reddish-brown, and determines the transparent or opaque character of the dots in the leaf. In rare cases there are no contents in the secretory cavities, which then only appear as dull transparent dots. Other features worth noting are that it is not a rare occurrence for the secretory cavities to be crowded at the margin of the leaf and that they are not always round, but may sometimes (*Maesa*, *Grammadenia parasitica*) have an elongated, sac-like shape. The resin-cavities are said to be accompanied by large spherical secretory cells in the leaf of *Cybianthus cuneifolius*, Mart. and *C. detergens*, Mart. (Bokorny) It may be added that secretory cavities are also present in the axis, where they are developed as canals, occurring either in the pith and primary cortex or in the latter alone [2]. In *Maesa indica*, Wall., resin-cells have been observed accompanying the secretory cavities in the pith [3].

Internal secretory organs of quite a peculiar type have been recorded by Höhnel in the leaf of *Ardisia crenulata*, and were described as 'proteid-containing glands' and 'fused secretory sacs.' The proteid-containing glands are visible even to the naked eye as oblong swellings on the crenate margin of the leaf and bear a certain relation to the marginal veins. In that portion of the leaf-margin which is devoid of glands, the marginal veins in transverse section consist of a ring of vascular bundles, surrounding a pith and developed more strongly towards the lower than towards the upper side of the leaf. In the neighbourhood of the gland, the upper part of this vascular ring becomes less developed and finally quite reduced. The gland itself is formed by the mass of pith, from which it appears to originate after the manner of an intramural gland, the cells of the pith appearing for the most part separated from one another, and only remaining united in such a way as to form long threads, filled with the secretion, which traverse the enlarged medullary cavity. This secretion is also very peculiar; even in the living leaf it consists of small bacteria-like bodies, which have the appearance of a precipitate and are shown by their chemical properties to be of the nature of proteid. 'Fused secretory sacs' occur in the leaf of *Ardisia crenata*, where they accompany secretory cavities. Each of these sacs has the appearance of a secretory cell enclosing a sphaero-crystal of variable size; from a study of the development, however, it becomes evident that each of them arises by fusion from a group of twenty or more cells. In the cells of such a group separate sphaero-crystals at first appear, but these gradually increase in size and coalesce to form a single round sphaero-crystal; thereupon the cell-walls lying within the secretory mass

[1] Bokorny was uncertain as to the nature of the secretory receptacles in *Maesa*. Radlkofer eliminated Bokorny's exceptions relating to the absence of the secretory cavities, for he demonstrated their presence in small numbers in *Cybianthus fuscus*, Mart. and showed that *Myrsine mitis*, Spreng. was a member of the Sapotaceae and *M. marginata*, Hook. et Arn. a member of the Ilicineae.

[2] Secretory cavities have been observed in the axis of certain species of *Myrsine*, *Cybianthus*, *Choripetalum*, *Ardisia*, *Maesa* and *Aegiceras*.

[3] The secretory cavities are wanting in the root of the Myrsineae (Van Tieghem).

become dissolved, while the peripheral walls are retained and surround the sphaero-crystal as a uniform envelope.

While the two tribes Maeseae and Eumyrsineae are distinguished from the Theophrasteae by the presence of secretory cavities, another interesting anatomical character appears in the latter tribe, although wanting in the remaining tribes of the Order. According to Vesque and Radlkofer, sclerenchymatous fibres are found beneath the epidermis on both sides of the leaf in *Theophrasta*, *Clavija*, *Deherainia* and *Jacquinia* [1]; in the two genera named first, they run approximately in the direction of the lateral veins, and are frequently so distinct in the dried leaf that they had previously attracted the attention of descriptive botanists, e. g. A. de Candolle and Decaisne.

According to Radlkofer, these fibres present features which are quite different in the four genera. In *Theophrasta* they have thick walls and narrow lumina, and are crowded together into stout, many-layered bundles of 36–64 or more fibres. These bundles have a tortuous course, somewhat like the bundles of fibres in the bast of the lime tree, and they anastomose, leaving meshes between them, which are occupied by green leaf-tissue. In the living leaf these bundles are scarcely noticeable, but in the dried leaf they project slightly externally, and give the upper surface of the leaf a peculiar sheen like satin; at the same time they prevent the network of veins from showing distinctly. In the species of *Clavija* the fibres have thinner walls and rather wide lumina. In this genus there is usually only a double layer of fibres and they are less distinct from the neighbouring elements, because a layer of hypodermal cells, elongated in the same direction, though having relatively thin walls, is not uncommonly to be found beneath the epidermis, at any rate on the upper side of the leaf. The sclerenchymatous fibres in question are in some cases so inconspicuous among the hypodermal cells that when the leaf is examined with a lens they may appear to be absent; in other species, however, they may be seen with a lens. These fibres do not prevent the network of veins from being evident in the dried leaf, and this is a very essential point. In *Deherainia* the fibres are widely separated from one another on the upper side of the leaf, and are arranged, several one above another, in a single or double row, but on the lower side of the leaf they are grouped together in large bundles. Their course approximately corresponds with that of the lateral veins. The essential character of the fibres of *Jacquinia* is their tendency to run in the direction of the midrib of the leaf. Other details vary within the genus, and these will render valuable services in a future revision of the species. In some species of *Jacquinia* (*J. ruscifolia*, Jacq., *J. aurantiaca*, Ait.) the fibres form a continuous, single, or locally double or triple subepidermal layer on the upper side of the leaf; in other species, however (*J. armillaris*, Jacq., *J. Berterii*, Spreng.), they form larger bundles, similar to those of *Theophrasta*. On the lower side of the leaf they are invariably arranged, as in *Deherainia*, in rather large isolated bundles.

The following facts may be mentioned with regard to the **hairy covering**. Simple uniseriate hairs are rare. In *Deherainia smaragdina* and *Jacquinia macrocarpa* they consist of a few, considerably thickened, cells (Vesque). *Jacquinia armillaris*, Jacq. (Fig. 116, *C*) has hairs of quite a peculiar type. These have a uniseriate stalk and a multicellular terminal portion, which is fantastically shaped and often branched; all the cells of the hair have sclerosed walls. The trichomes in question cover the shoots so densely that their true nature does not become evident until one examines thin sections, the surface of the shoots appearing granulated, not hairy. The capitate or peltate trichomes are much more important than those so far discussed; some of them have solely a clothing function, but others are glandular. Their head or shield, as the case may be, is divided by vertical walls only. Such trichomes are described by Vesque as occurring in species of *Myrsine*, *Ardisia*, *Jacquinia*, *Clavija* and *Theophrasta*, by O. Bachmann in species of *Ardisia*, *Conomorpha* and *Hymenandra*, by

[1] According to Radlkofer the genus *Reptonia*, cited amongst the Theophrasteae in Durand's Index and in the Natürl. Pflanzenfam., is not a member of the Myrsineae, but belongs to the Sapotaceae.

Radlkofer in all four genera of the Theophrasteae, i. e. for *Deherainia* as well; they also occur in *Aegiceras*, according to a casual observation of my own.

The following points regarding the structure of these capitate and peltate hairs are based principally on my own observations, since many of the statements in the literature are too indefinitely expressed to be further considered. *Ardisia japonica*, *A*. DC. (Fig. 116, *D*) has peltate hairs with a clothing function; they are composed of a short and broad stalk-cell and of a rather large shield, which has a slightly lobed margin; only certain of the ray-cells reach to the centre of the shield, and it is exceedingly rare for them to be divided by a tangential wall. Precisely similar trichomes are also found in *Ardisia polyneura*, Miq., *Conomorpha*

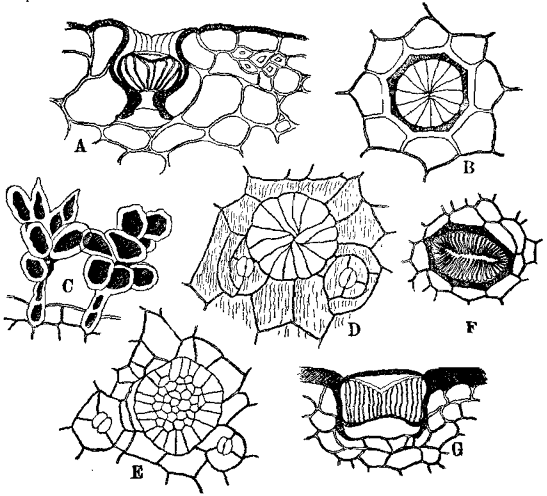

FIG. 116. Hairy covering of the Myrsineae: A–B, Depressed glandular hair of *Clavija caloneura*, Mart., A, in transverse section, B, in surface-view. C, Hairs from the surface of a branch of *Jacquinia armillaris*, Jacq. D, Peltate hair of *Ardisia javanica*, A. DC. E, Peltate hair of *Ardisia macrocarpa*, Wall. F–G, Glands of *Aegiceras majus*, Gärtn.—Original.

macrophylla, Mart., and *C. heterantha*, Benth., according to O. Bachmann. The peltate hairs of *Ardisia macrocarpa*, Wall. (Fig. 116, *E*), and other species of *Ardisia*, of *Conomorpha nemoralis*, Mart. et Miq., and *Hymenandra Wallichii*, A. DC. have a glandular function; upon the stalk-cell is seated a shield of relatively small circumference, and showing a large number of 4- or more-sided cells in surface-view; these at first sight appear to be irregularly arranged, but they can in many cases be referred to ray-cells, which start from a median line in the shield and are subdivided by radial and tangential walls. The capitate hairs of the four genera of the Theophrasteae also have a glandular function; they are deeply sunk in the surface of the leaf and thus cause the depressed dots, which long ago attracted the attention of systematists (see A. de Candolle and Bentham and Hooker). The hairs (Fig. 116, *A–B*) consist of a basal cell, a short stalk-cell, and a flatly arched head; the narrow ray-cells of the latter are present in varying numbers,

arranged radially or approximately so in surface-view, and appear like palisade-cells in a transverse section of the leaf; usually the head alone is raised above the base of the depression. Outside the group Theophrasteae, similar depressed glandular capitate hairs occur in *Myrsine capitellata*, according to Vesque, and in *Aegiceras*, according to my own observation. The glandular hairs of *Aegiceras* (Fig. 116, *F–G*) are especially peculiar in having their lateral walls almost fused with the wall of the depression, and in the arrangement of the ray-cells in surface-view, which reminds one of certain corals (*Cyclolithes* or *Fungia discus*).

3. Structure of the Axis. This has hitherto been little investigated. The following statements regarding the structure of the **wood** are based on an examination of *Maesa Doraena*, Bl., *M. indica*, Wall., *Ardisia crenulata*, Vent., *Myrsine umbellata*, Mart., *M. semiserrata*, Wall., *Clavija macrophylla*, Miq. var. and *Jacquinia armillaris*, Jacq. The medullary rays vary in breadth, being as much as six cells broad in *Ardisia crenulata*, as much as three in *Maesa Doraena*. Their cells are usually elongated in the vertical direction; this is frequently the case even when the medullary rays are broad, although in other instances the cells of such medullary rays are radially elongated. The vessels never have specially wide lumina. The wood in the branches of *Jacquinia armillaris* lacks secondary medullary rays, and is also distinguished by being poorly supplied with vessels. According to my observations, the walls of the vessels bear bordered pits only, even where they are in contact with parenchyma; Pomrencke states that both bordered and simple pits occur on these parts of the wall in the wood of the stem in some species of *Myrsine*. Spiral thickening of the vessel-wall is found in *Maesa Doraena*. The perforations of the vessels are chiefly simple in the species investigated by me. In *Maesa Doraena*, *M. indica*, and *Ardisia crenulata*, scalariform perforations are found accompanying those of the simple type, and in *Ardisia* they even have numerous bars. In wood from the stems of species of *Myrsine*, Pomrencke found both simple and scalariform perforations or only one of these two types. Pomrencke mentions the occurrence of an excretion of carbonate of lime in the lumina of the vessels in *Myrsine Grisebachii*, Hieron. The wood-parenchyma does not take a prominent part in the formation of the xylem-mass in any member of the Order. The wood-prosenchyma has moderately thick walls and rather wide lumina and bears simple pits; the lumen is, to a certain extent, septate in all the species mentioned above except *Jacquinia armillaris*.

As no statements on the subject were to be found in the literature[1], I investigated the structure of the **cortex** in *Maesa Doraena*, Bl., *Myrsine umbellata*, Mart., *Jacquinia armillaris*, Jacq., *Deherainia smaragdina*, Decne., and *Clavija macrophylla*, Miq. var. The formation of cork is superficial, being subepidermal in *Maesa*, *Myrsine*, and *Jacquinia*, epidermal in *Clavija*. In *Jacquinia armillaris* it consists of sclerosed cells with peculiar, doubly refracting contents. The pericycle contains isolated arcs of sclerenchymatous fibres in *Clavija*, an almost closed ring of sclerenchyma in *Maesa*, and a continuous and composite ring in the remaining species. The sclerenchymatous fibres of the pericycle differ from typical bast-fibres in not having pointed ends or abundant pitting. The primary cortex sometimes, e.g. in *Clavija macrophylla* and *Jacquinia armillaris*, contains stone-cells.

The secretory organs of the axis have already been dealt with above (see structure of the leaf).

Literature: Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 62 and 358.—De Bary, Vergl. Anat., 1877.—Höhnel, Sekretionsorg., Sitz.-Ber. Wiener Akad., Bd. lxxxiv, Abt. 1, pp. 574 and 583 et seq.—Szyszylowicz, Beh. flücht. Oele (Polish), Pamietnik Akad. Umiejetn. W. Krakowie, t. vi, 1881, p. 23 et seq. and Tab. vi, vii.—Bokorny, Durchs. P., Flora 1882, p. 373 et seq., separate

[1] *Theophrasta imperialis*, Hort., described in Möller's 'Baumrinden' under Myrsineae, is a member of the Sapotaceae (*Chrysophyllum imperiale*).

copy, pp. 27–31.—Van Tieghem, in Ann. sc. nat., sér. 7, t. i, 1885, pp. 57, 58.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. i, 1885, pp. 245–54 and pl. 12.—Solereder, Holzstr., 1885, pp. 165–7.—O. Bachmann, Schildhaare, Flora 1886, separate copy, pp. 19, 20 and Tab. ix.—Radlkofer, Durchs. P., Sitz-Ber. Münch. Akad. 1889, pp. 321, 322.—Leblois, Can. sécrét. etc., Ann. sc. nat. sér. 7, t. vi. 1887, pp. 272, 273.—Radlkofer, *Theophrasta* &c., Sitz.-Ber. Münch. Akad. 1889, p. 238 et seq.—Pax, in Natürl. Pflanzenfam., iv. Teil, Abt. 1, 1889, p. 85 et seq.—Schimper, Indomalay. Strandpfl., 1891, p. 17 and Tab. iv.—Pomrencke, Holz einig. symp. Fam., Prantl, Arb. bot. Garten Breslau, 1892, p. 43 et seq.—Mattej, Corpuscoli rossi &c., Boll. Soc. bot. Ital. 1897, p. 83 et seq.

SAPOTACEAE.

There are two anatomical features, which, taken together, enable one to recognize any member of the Sapotaceae even in the sterile condition, and are thus specially characteristic of the whole Order: firstly, the occurrence of unicellular, two-armed hairs, and secondly, the presence of rows of laticiferous sacs, which are found in the leaf, for the most part accompanying the veins, and are also met with in the axis (in pith and cortex). Except for the two-armed hairs, which are sometimes modified into one-armed hairs, no other form of trichome occurs. To the two anatomical characters mentioned we can add a third, viz. the occurrence of irregularly shaped, doubly refracting masses of caoutchouc, which vary in size and are to be found in dried material in the assimilatory tissue of every full-grown Sapotaceous leaf; and a fourth character, viz. the lack of a special uniform type of stoma in nearly all cases. In the structure of the axis, the following characters are of value for the diagnosis of the Order: as far as is known, the formation of cork is superficial; the wood-parenchyma is developed so as to form tangential bands, and the wood-prosenchyma has simple pits. The perforations of the vessels show a tendency towards a scalariform differentiation. The vessel-wall, where it is in contact with parenchyma of the medullary rays, bears large, simple, elliptical pits side by side with bordered pits. Oxalate of lime is deposited in the form of solitary or clustered crystals, while in the laticiferous sacs it is frequently found in the form of finely granular crystal-sand.

The structure of the leaf has been specially examined by Holle in continuation of Vesque's general comparative statements. Holle's investigations extended to comprehensive material, which had been critically revised by Radlkofer, and in the endeavour to obtain specific and generic characters for the systematic rearrangement of the Order they have yielded numerous details, of which only the most important can be quoted here[1]. The structure of the leaf-tissue is bifacial; a tendency to centric structure occurs in isolated cases only. The palisade-tissue consists of one or more layers; occasionally the number of layers has determinative value for groups of species. The spongy tissue is, in most cases, loose and provided with large intercellular spaces; more rarely it is dense. The structure of the **epidermis** of the leaf varies greatly. The cuticle, especially on the lower surface of the leaf, commonly shows irregularities such as granulation, striation, and formation of ridges or comb-like structures. The latter (Fig. 117) resemble mountain ranges in a surface-view of the leaf, and in a transverse section appear as prongs or rods, which vary in size and are often branched. They are specially well developed on the lower side of the leaf in all species of the genus *Oxythece*. The outer and lateral walls of the epidermal cells vary in thickness, the latter being straight or undulated. Marginal pits are not uncommon. Formation of papillae on the lower epidermis has not been observed in any member of the Order, and gelatinization of the epidermal cells has only been seen in three species

[1] The specific nomenclature made use of here is that of Holle; with regard to this point see Holle, loc. cit., p. 8.

(*Dipholis salicifolia*, A. DC., *D. montana*, Griseb., and *Bumelia cubensis*, Griseb., β. *oblongata*, Griseb.). In *Chrysophyllum Cainito*, L. the cells of the upper epidermis of the leaf are divided by one or more transverse walls. This is suggestive of a transition to the differentiation of a **hypoderm**, which appears in many members of the Order. Hypoderm is either characteristic of an entire genus (e.g. *Illipe*, F. v. Müll.) or of certain sections of a genus (e.g. the sections *Calvaria*, Radlk. MS. and *Mermularia*, Radlk. MS. of the genus *Sideroxylon* and the section *Antholucuma* of the genus *Vitellaria*, Gärtn. fil. emend. Radlk.) or only of certain species (species of *Bumelia*, *Mimusops*, *Dipholis* and *Chrysophyllum*). The details of the differentiation of the hypoderm (development on one or both sides of the leaf, number of layers, shape, and size of its cells and structure of their walls) show numerous variations, which are of value for specific diagnosis. The **stomata** in nearly all cases are found only on the lower surface of the leaf. According to Holle, there are only two members of the Order (*Omphalocarpum*, sp. cult. Hort. Monac. and Balansa's plant n. 2390 from Paraguay) in which they are present in large numbers on the upper side also, whilst in *Ecclinusa costata*, Pierre, and *E. ramiflora*, Mart., isolated stomata have been met with on the upper surface. As a rule, the stomata are surrounded by 3–4 epidermal cells; only in a few species (*Pradosia lactescens*, Radlk. and *Rhamnolucuma novocaledonica*, Baill.) are all the stomata accompanied by subsidiary cells placed parallel to the pore, while this type is associated with the commoner form, though less abundant than the latter, in some species of *Chrysophyllum* and in *Iteiluma Baillonii*, Baill. Usually the guard-cells lie in the same plane as the epidermal cells; but depressed stomata, which are often very considerably sunk (e.g. in *Pouteria ramiflora*, Radlk. and the species of the two sections *Calvaria*, Radlk. MS. and *Mermularia*, Radlk. MS. of the genus *Sideroxylon*), also occur; it is rare for the stomata to be elevated (*Sarcosperma* and *Mimusops Caffra*, E. Mey.). The smaller **veins** of the leaf may be either vertically transcurrent (by means of sclerenchyma or collenchyma) or embedded; their vascular bundles are usually accompanied by sclerenchyma in both cases. The occurrence of sclerenchymatous fibres in the mesophyll is very widely distributed in the Order. Holle describes them as being present in the following cases: *Chrysophyllum glabrum*, Jacq., all the species of the section *Caloneuron*, Radlk. MS., certain species belonging to the section *Chrysalidops*, Radlk. of the genus *Micropholis*, and certain species of *Payena*, *Bumelia*, *Mimusops*, *Oxythece*, *Pachystela*, *Achras*, *Ecclinusa*, *Passaveria*, *Labourdounaisia*, *Sersalisia*, *Lucuma*, *Iteiluma*, *Amorphospermum*, *Labramia*, *Elaeoluma*, and *Gymnoluma*. These sclerenchymatous fibres generally have a thick wall and a narrow lumen, but moderately thick fibres with wide lumina have been met with in *Chrysophyllum glabrum*; spirally thickened fibres occur in the species of *Micropholis* belonging to the section *Caloneuron*. For the varied course of the sclerenchymatous fibres, see Holle, loc. cit.

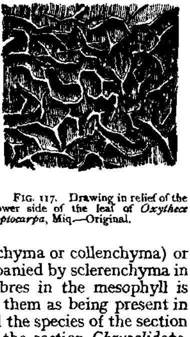

FIG. 117. Drawing in relief of the lower side of the leaf of *Oxythece leptocarpa*, Miq.—Original.

The **hairy covering** on all parts of the plant consists, as has already been pointed out above, exclusively of unicellular two-armed trichomes, which may sometimes (*Calocarpum mammosum*, Pierre) pass over into one-armed hairs in consequence of the reduction of one arm. Occasionally these hairs have only a clothing function; in many cases, however, they are also glandular in nature, as is proved by the excretion of resin, which frequently covers the lower side of leaves bearing a dense hairy covering. The two-armed

hairs vary in the nature of their walls, which may be thin or strongly thickened, the thickening in the latter case being sometimes confined to the lower wall in both arms; other differences are shown in: (*a*) the length of the arms (thus there are hairs with very long arms in most species of *Chrysophyllum* and in *Planchonella*, hairs with short arms in *Oxythece*, *Passaveria*, *Pradosia*, *Payena*, &c.); (*b*) the shape of the hairs (Y-shaped hairs in *Calocarpum mammosum*, Pierre, and others resembling a boot-jack—in consequence of the forking of one arm of the hair—in *Cryptocoryne Gerrardiana*, Hook.); and (*c*) the colour of the hairs, which is golden-yellow, rusty-brown or silvery white. The short stalk is part of the single cell forming the hair and is occasionally (especially in *Labatia*) surrounded by subsidiary cells, which sheathe the stalk-portion and are more strongly thickened where they are in contact with it; in consequence of this, characteristic scars are produced when the hairs fall off.

Oxalate of lime occurs in the form of ordinary solitary and clustered crystals and also as crystal-sand. Typical crystal-sand is only found intermingled with the latex; but a few crystalline granules are sometimes present accompanying large solitary crystals in the same cell. The clustered crystals may occur alone in the leaf (species of *Sideroxylon*, belonging to the section *Calvaria*), or there may be only solitary crystals (*Mimusops*, species of *Sideroxylon*, belonging to the section *Mermularia*), or both types together. The clustered and solitary crystals are found both in the integumental and in the assimilatory tissue; only solitary crystals have been observed accompanying the sclerenchyma of the veins.

According to Holle, the position in which the crystalline elements occur in the leaf is of systematic value, as is shown by the following examples. In *Pradosia* rather large solitary crystals are met with in correspondingly large cells of the palisade-tissue; the entire mesophyll in *Reptonia buxifolia*, A. DC. contains large cells occupied by solitary crystals; in *Labatia* certain cells of the palisade-tissue which are subdivided by transverse walls contain single crystals in the compartments; in *Elaeoluma* solitary crystals occur in the lower epidermis of the leaf; in *Rhamnoluma caledonica*, H. Baill. and other cases, in the hypoderm. In *Palaquium ellipticum*, Engl., the clustered crystals are enclosed in enlarged cells of the palisade-tissue; *Palaquium grande* has clustered crystals in the mesophyll and in the lower epidermis of the leaf; the position of the clustered crystals varies greatly in the different species of *Bumelia*, where they are either to be found in the uppermost or in the lowermost layer of the mesophyll or in these two layers as well as in an intermediate mesophyll-layer, and so on.

The **laticiferous sacs** characteristic of the Order are present in the axis and leaf, and are invariably arranged in rows. In the axis they are found in the pith, bast and primary cortex; in the leaf they usually accompany the vascular system of the veins. In transverse sections of the leaf one occasionally finds laticiferous sacs which are apparently independent of the vascular strands of the veins; this is mostly due to the fact that in the neighbourhood of the angles formed by the veins, the rows of laticiferous sacs not uncommonly leave the vascular system, as it were, cutting across the angle; they thus traverse the mesophyll for the distance of a few cells, and finally attach themselves again to the strand of the vein. Laticiferous sacs which are really free in the mesophyll are rare (*Donella Roxburghiana*, Pierre and *Amorphospermum antilogum*, F. v. Müll.). In the axis the individual laticiferous sacs are of varying length, and also vary greatly in diameter. Those situated in the leaf do not possess a large lumen but show distinct elongation, which varies in degree. The wall of these elements is not suberized and is generally closed on all sides; Holle has demonstrated the occurrence of vessel-like connexions in the laticiferous sacs of the primary cortex of *Sapota Pohlmaniana*, F. v. Müll. (in the form of circular holes), and Vesque has shown

that the same features occur in the leaf of *Bumelia*. The contents of the laticiferous sacs are in part doubly refractive, and are formed essentially by resinous and caoutchouc-like substances, which are mostly soluble in chloroform, benzol, and carbon disulphide. These substances are sometimes accompanied by crystal-sand, consisting of oxalate of lime according to Holle and Leschwin [1], and starch (*Bassia latifolia*, Roxb.) according to Heckel and Schlagdenhauffen.

The structure of the **wood** has been examined [2] by Möller, Molisch, Pomrencke, and myself. In the branches the medullary rays are mostly 1–2-seriate, rarely 4-seriate; they are broader throughout the wood of the main stem (4–6-seriate). The diameter of the vessels varies (max. diam. = ·075 mm. in *Mimusops Imbricaria*). The perforations of the vessels are chiefly simple; accompanying this type, scalariform perforations with 1–7 bars have been observed in the species investigated by me and in *Lucuma Cainito* and *Chrysophyllum lucumifolium*, according to Pomrencke. In the species which I examined, the vessel-wall, where it is in contact with parenchyma of the medullary rays, has large, elliptical, simple pits in addition to bordered pits. The wood-parenchyma is rather strongly developed, and forms tangential bands of varied thickness in transverse sections of the branch. The wood-prosenchyma has thick walls and narrow lumina, and is provided with simple pits.

Regarding the structure of the **cortex**, the small amount of information contained in Möller's 'Baumrinden' [3] is practically all that is known. The cork arises superficially, in the first cell-layer of the primary cortex (*Achras*, *Lucuma; Chrysophyllum pyriforme*, according to Douliot) or in the second, third or fourth layer (*Sapota*). The later internal periderms are distinguished by the prevalent sclerosis of the inner walls of the cork-cells in all the species examined. In the cortex of the branches of *Sapota* and *Lucuma*, isolated groups of hard bast are present in the pericycle. The cortex of *Monesia* is distinguished by the structure of the secondary bast, owing to its lack of bast-fibres and the development of groups of stone-cells; the rest of the 'barks' belonging to this Order have secondary hard bast. Oxalate of lime occurs in the form of solitary crystals contained in chambered fibres, which accompany the bundles of bast-fibres. Mention has already been made of the laticiferous sacs of the cortex.

Literature: Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 62, 63 and 358.—De Bary, Vergl. Anat., 1877, especially pp. 158–60.—Molisch, Vergl. Anat. d. Holzes d. Ebenac. etc., Sitz.-Ber. Wiener Akad., Bd. lxiii, Abt. 1, 1879, p. 54 et seq.—Möller, Rindenanat., 1882, pp. 192–200.—Radlkofer, in Sitz.-Ber. Münch. Akad. 1882, p. 265 et seq. and 1884, pp. 397 and 437 et seq.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. i, 1885, pp. 255–63 and pl. 12.—Solereder, Holzstr., 1885, pp. 167, 168.—Heckel and Schlagdenhauffen, in Compt. rend., t. cvii, 1888, pp. 949–53.—Radlkofer, in Sitz.-Ber. Münch. Akad. 1888, p. 405 et seq. and 1889, p. 265 et seq.—Dehmel, Milchsaftbeh., Diss., Erlangen, 1889, p. 30 et seq.—Douliot, in Ann. sc. nat., sér. 7, t. x, 1889, p. 375.—Engler, in Natürl. Pflanzenfam., iv. Teil, Abt. 1, 1890, p. 127.—Holle, Anat. Bau d. Blattes d. S., Diss., Erlangen, 1892, 59 pp. and 1 Tab.—Pomrencke, in Arb. bot. Gart. Breslau, 1892, pp. 47–9.—Oesterle, *Guttapercha*, Diss., Bern, 1893.—Leschwin, Z. pharm.-hist. Kenntn. von *Palaquium Gutta* &c., Mag.-Diss., Petersburg, 1894, Russian; abstr. in Pharm. Post, Wien, 1894, n. 35.—Chimani, Milchröhren, Bot. Centralbl. 1895, i, p. 305 et seq.

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[1] Chimani, to whom Holle's work was unknown, wrongly criticizes Leschwin's statement in the following words (l. c., p. 419): 'This statement can only be due to a mistake!'

[2] The following plants were investigated by Möller: *Mimusops Imbricaria*, L. and *Sideroxylon cinereum*, Lam.; by Molisch five species of the genera *Achras*, *Sideroxylon*, *Bassia*, *Chrysophyllum* and *Sapota*; by Pomrencke *Lucuma Cainito*, A. DC., *L. neriifolia*, Hook. et Arn., *Chrysophyllum lucumifolium*, Griseb., *Bumelia obtusifolia*, R. et Sch., *B. cuneata*, Sw.; by me *Bassia latifolia*, Roxb., *Isonandra lanceolata*, Wight and *Payena lucida*, DC.

[3] The following plants have been investigated: *Monesia*-bark = *Pradosia lactescens*, Radlk., *Sideroxylon borbonicum*, A. DC., *Achras Sapota*, L., '*Sapota Mülleri*, Lind.,' *Lucuma Cainito*, R. et Sch., *L. procera*, Mart., *Mimusops Elengi*, L., *M. hexandra*, Roxb. and *Imbricaria maxima*, Poir.

EBENACEAE.

1. Review of the Anatomical Features. There are no special anatomical characters common to the whole Order. The laticiferous sacs characteristic of the nearly related Sapotaceae are wanting. The structure of the wood is uniform. All the genera (with the exception of the anomalous genus *Brachynema*) have simple perforations in their vessels. The medullary rays of the wood are narrow; the vessel-wall bears bordered pits, even where it is in contact with parenchyma of the medullary rays; the wood-parenchyma is developed in moderate abundance, and traverses the wood in the form of tangential bands; the wood-prosenchyma is provided with small, but distinctly bordered pits. The structure of the cortex shows essential differences in the individual genera. The origin of the cork is subepidermal in *Maba*, *Diospyros*, and *Tetraclis*, in which a sclerenchymatous ring is present at the outer limit of the bast; in *Royena* and *Euclea*, however, the cork develops in the pericyclic region, and in these genera the cork-cambium produces a sclerotic phelloderm, while the continuous ring of mechanical tissue in the pericycle is wanting. Development of secondary bast-fibres does not appear to take place in this Order, although parenchymatous sclerenchyma may occasionally be observed in the secondary bast. The leaf-structure is mostly bifacial; the stomata are surrounded by a varying number of ordinary epidermal cells; gelatinization of the epidermis has not been observed, and hypoderm rarely occurs. Stone-cells commonly occur in the parenchyma of the petiole and of the veins; they are rarer in the mesophyll (species of *Euclea*, *Diospyros*, and *Maba*). The occurrence of large solitary crystals in correspondingly large cells of the mesophyll is characteristic of many members of the Order, though not of all. Oxalate of lime occurs not only in the form of solitary, but also in that of clustered crystals. The hairy covering consists, for the most part, of simple, unicellular hairs, which are very rarely combined to form tufted hairs. In addition to these, unicellular two-armed trichomes (*Diospyros*) and glandular hairs (Fig. 118, *C*) occur. The latter are small and club-shaped; their curved uniseriate stalk usually merges gradually into the glandular head, which is made up of a few cells. Besides the features already touched upon, the occurrence of papillae on the lower surface of the leaf (Fig. 118, *A–B*) and the varied structure of the veins of the leaf may be mentioned as suitable for specific diagnosis.

The anatomy of the anomalous genus *Brachynema* differs essentially from that of the remaining genera in the exclusive occurrence of scalariform perforations in the vessels and the presence of large, simple pits on the vessel-wall, where it is in contact with parenchyma; the wood-prosenchyma has bordered pits in *Brachynema*, as in the other members of the Order.

2. Structure of the Leaf. In addition to Vesque's general comparative statements on this subject, there is a detailed treatise by Parmentier; this is based on the examination of ten species of *Royena*, thirteen species of *Euclea*, twenty-six of *Maba*, about seventy of *Diospyros*, and the monotypic genus *Tetraclis*.

The general features of the leaf-structure may be noticed first. The mesophyll is bifacial in most cases. In some species of *Royena*, *Diospyros*, and *Euclea*, subcentric structure occurs, and the leaf is distinctly centric in *Euclea pseudebenus*, E. Mey. and *Royena glabra*, L. The epidermal cells usually have undulated or, more rarely, straight lateral walls. The thickness of the outer wall varies greatly; the cuticle is sometimes striated. Gelatinization of the epidermal cells has not been observed in any member of the Order. A specially noteworthy feature is the papillose differentiation of the lower epidermal cells, the cell-lumen often scarcely taking any part in the formation

of the papillae. These papillae are found in certain species of *Diospyros* and *Maba*, viz. *Diospyros cargillia*, F. v. Müll., *D. pentamera*, Woolls. et F. v. Müll., *D. discolor*, Willd. (Fig. 118, *A–B*), *D. argentea*, Griff., and *Maba sericea*, Hiern. The **stomata**, which almost always have rather a wide front cavity, are surrounded by several epidermal cells which have no special orientation. They may be either depressed or raised above the level of the epidermis, or may be on the same level as the latter. They are mostly confined to the lower side of the leaf; in *Euclea pseudebenus*, E. Mey., however, they occur on both sides. Hypoderm is very rare in this Order; Parmentier observed it as a single layer on both sides of the leaf of *Maba humilis*, R. Br. The palisade and spongy tissue vary in their differentiation; the latter is sometimes dense, sometimes very lacunar. The smaller **veins** also show various structural features, which, like the majority of the characters so far referred to, are only of value for specific diagnosis. In most cases their vascular bundles are accompanied by sclerenchyma, which often attains a considerable development. The veins may be either vertically transcurrent or embedded, but this character also is only valid for species. Small veins which are vertically transcurrent by means of colourless parenchyma, however, occur in most species of *Diospyros*. The sclerosed parenchymatous cells of the mesophyll form a special feature. In very many species of *Diospyros* and *Maba* and also in *Euclea polyandra*, E. Mey. stone-cells

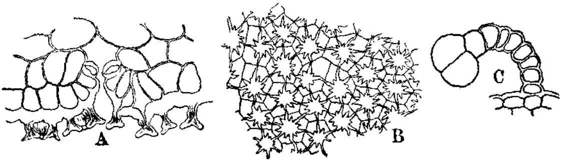

FIG. 118. A–B, Papillose epidermis of the lower side of the leaf in *Diospyros discolor*, Willd.; A in a transverse section B, in surface-view. C, Glandular hair of *Diospyros Kaki*, L.f.—Original.

are present in the parenchyma of the petiole or of the veins; regarding their distribution Parmentier's work may be referred to. The occurrence of sclerosed and sometimes slightly branched cells in the mesophyll, especially in the palisade-tissue, is more important from a systematic point of view; these cells are found in the following species: *Diospyros acuta*, Thw., *D. argentea*, Griff., *D. discolor*, Willd., *D. emarginata*, Hiern, *D. eriantha*, Champ., *D. gaultheriaefolia*, Mart., *D. peruviana*, Hiern, *D. Poeppigiana*, A. DC., *D. Weddelii*, Hiern, *Maba Hilairei*, Hiern, *M. sandwicensis* A. DC., and *M. sericea*, Hiern.

Oxalate of lime occurs chiefly in the form of solitary crystals, rarely (species of *Diospyros, Maba, Royena, Tetraclis*) in the form of clustered crystals. In very many species of *Diospyros, Maba*, and *Royena*, large solitary crystals are found in correspondingly large cells of the mesophyll ('cristaux d'illumination' of Parmentier) and occasionally give rise to transparent dots in the leaf [1]. Numerous crystalline granules sometimes (*Diospyros discolor*, Willd.) accompany the solitary crystals in the same cell. Internal secretory receptacles are wanting in this Order.

The **hairy covering** consists of clothing and glandular hairs. The clothing hairs are (*a*) ordinary unicellular trichomes, by the juxtaposition of which tufted hairs (*Royena hirsuta*, L.) originate, and (*b*) unicellular malpighian hairs with

[1] It remains to be determined whether the pellucid dots mentioned by Hiern (Monogr. of Eben., 1873, p. 136) in his *Maba punctata* are caused by crystal-cells of this kind.

one long and one very short arm (in *Diospyros argentea*, Griff., *D. cauliflora*, Bl., *D. discolor*, Willd., &c.[1]). Glandular hairs have hitherto rarely been observed—by Vesque and Parmentier in a few species of *Diospyros* and by me in *Royena pubescens*, Willd. It is possible that they are only readily recognizable on the young leaves. The glandular hairs (Fig. 118, *C*) are small and club-shaped. They have a curved, uniseriate stalk, composed of a small number of cells, and a head which is unicellular or composed of a few cells and which is more or less distinctly marked off from the stalk ; when the head consists of a few cells it is either divided by horizontal and vertical walls or by vertical walls only.

A description of the leaf-structure of the monotypic Brasilian genus *Brachynema* (with *B. ramiflorum*, Benth., Spruce, Brasilia) follows ; Hiern is probably right in excluding this plant from the Ebenaceae ; in Bentham and Hooker, as also in Durand's Index, it is appended to this Order as a doubtful member. The leaf of *Brachynema* has bifacial structure. The lateral walls of the epidermal cells are fairly straight. The stomata have three subsidiary cells and occur only on the lower surface of the leaf. The vascular bundles of the veins are surrounded by a sclerenchymatous ring. It is especially noteworthy that the sclerenchyma of the veins is accompanied by numerous cells containing relatively small solitary crystals ; the crystals are inserted in sclerotic thickenings on the walls bordering on the sclerenchyma. Glandular hairs are absent.

3. Structure of the Axis. The structure of the axis, like that of the leaf, is well known, since all the genera have been investigated by Molisch, Möller, Solereder, and Parmentier.

The structure of the **wood** presents the following important features. The medullary rays are not broad, being 1–2-seriate, or at the most 3-seriate. According to Höhnel, the medullary rays in the wood of the stem of *Diospyros virginiana*, L. exhibit a tier-like structure. The vessels have lumina of very different sizes ; in *Diospyros discolor*, Willd., the diameter of the vessels reaches ·12 mm. The perforations of the vessels are simple throughout. Their walls have bordered pitting, even where they are in contact with parenchyma. The abundant development of wood-parenchyma is characteristic ; this tissue occurs in tangential bands, which are sometimes only one cell in breadth ; it traverses the tissue of the wood and also occurs in the neighbourhood of the vessels. The cells of the wood-parenchyma are not uncommonly septate (e.g. in *Euclea racemosa*, Thunb., *Diospyros chloroxylon*, Roxb. and *Maba buxifolia*, Pers.), and contain solitary crystals. The wood-prosenchyma has slit-like pits with a distinct though small border, which is often smaller than the slit.

It is perhaps well to mention here, that the heart-wood of certain species of *Diospyros* and *Maba* (*M. Ebenus*, Spreng.) constitutes what is called ebony, distinguished by its black colour. This colour is caused by black or brown contents, which fill the vessels and the lumina of the wood-prosenchyma. The recent investigations of Belohoubek have shown that part of the black contents of ebony wood are soluble in caustic potash and are due to humic acid, while the part that is insoluble in alkalies consists essentially of carbon. Molisch had already shown at an earlier date that the black contents arise by a process of humification from a gum originally present in the cell-lumen.

In the structure of the **cortex**, which Möller and Parmentier have investigated, we may notice first the development of the cork. In the genera *Maba*, *Diospyros*, and *Tetraclis*, the cork arises immediately below the epidermis, but in *Royena* and *Euclea* in the pericycle. In the last two genera, the cork-cambium forms a sclerotic phelloderm internally. According to Parmentier, the pericycle contains a sclerenchymatous ring in the

[1] Vesque's statement regarding the occurrence of simple uniseriate hairs in *Diospyros discolor* is incorrect.

three genera showing superficial development of cork (*Diospyros*, *Maba*, and *Tetraclis*); on the basis of what I have found in *D. Kaki*, L.f., it is probable that this ring is always composite and continuous. It is wanting in *Royena* and *Euclea*, in which sometimes, at any rate (as in *R. lucida*, L.), isolated groups of bast-fibres are developed in the pericycle. In the secondary bast Möller expressly mentions the absence of secondary bast-fibres, and the occurrence of spindle-shaped stone-cells in the case of *Diospyros*. Parmentier makes no reference to the occurrence of secondary hard bast in any of the numerous species investigated by him, so that one must probably assume that it is wanting in all the members of this Order.

The anomalous genus *Brachynema*, the leaf-structure of which has already been referred to above, differs essentially from the remaining genera in the structure of its axis. Thus the perforations of the vessels are exclusively scalariform, and the vessel-wall bears large, simple, elliptical pits where it is in contact with parenchyma of the medullary rays. Other features in the structure of the wood may also be mentioned: the medullary rays may be as much as four cells in breadth; the vessels do not have wide lumina, and the wood-prosenchyma has thick walls, rather wide lumina, and bordered pits. The pith is traversed by transverse plates of stone-cells. The inner part of the primary cortex contains a broad ring of stone-cells, while in the outer region cells with wide lumina filled with blood-red contents occur; these cells are arranged in vertical rows. The pericycle includes isolated bundles of bast-fibres. In the neighbourhood of the ring of stone-cells and of the bast-fibres there are crystal-cells of the same type as those accompanying the sclerenchyma of the veins. Cork was not present on the branches present in herbarium-material.

Literature: Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 63, 64 and 359.—Molisch, Vergl. Anat. d. Holzes d. E. etc., Sitz.-Ber. Wiener Akad., Bd. lxxx, Abt. 1, 1879, p. 65.—Möller, Rindenanat., 1882, pp. 200, 201.—Belohoubek, Ebenholz, Sitz.-Ber. k. böhm. Gesellsch. d. Wiss. in Prag 1883, p. 384 et seq.—Höhnel, Stockwerkart. Holzk., Sitz.-Ber. Wiener Akad., Bd. lxxxix, Abt. 1, 1884, p. 42.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. i, 1885, pp. 263-7 and pl. 13.—Solereder, Holzstr., 1885, pp. 168, 169.—Radlkofer, Durchs. P., Sitz.-Ber. Münch. Akad. 1886, p. 323.—J. E. Weiss, Korkbild., Denkschr. Regensb. bot. Gesellsch. 1890, separate copy, p. 57.—Gürke, in Natürl. Pflanzenfam., iv. Teil, Abt. 1, 1890, p. 154.—Pomrencke, Holz einig. symp. Fam., Arb. bot. Gart. Breslau 1892, pp. 49-51.—Parmentier, Hist. comp. des E., Paris, 1892, 155 pp. and 4 pl.

STYRACEAE.

The following features are of importance for the anatomical diagnosis of this Order. The wood contains vessels with perforations, which are usually exclusively scalariform, though rarely (*Diclidanthera*) simple, and wood-fibres, which always have bordered pits. The formation of cork is either internal and pericyclic (*Styrax*, *Pamphilia*, and *Halesia*) or superficial (*Diclidanthera* and *Symplocos*). In the structure of the leaf it is noteworthy that the stomata are not, as a rule, accompanied by any special subsidiary cells; *Symplocos* alone is distinguished by the possession of subsidiary cells which are placed parallel to the pore. Glandular hairs are absent, but in addition to simple uniseriate trichomes, stellate hairs, which in some cases show transitions to peltate scales, are widely distributed. Oxalate of lime is excreted in the form of ordinary solitary or clustered crystals.

The following remarks concerning the details of the **leaf-structure** are based on an investigation of *Symplocos adenophylla*, Wall., *Halesia tetraptera*, L., *Styrax camporum*, Pohl, *Pamphilia styraciflua*, DC., and *Diclidanthera laurifolia*, Mart. The structure of the leaf is bifacial in the cases examined. The cells of the epidermis have either undulated or straight lateral walls. Gelatinization of the epidermis has not been observed in any case. In *Symplocos adenophylla* the outer wall of the lower epidermis is distinctly striated. A one-layered hypoderm is developed beneath the upper epidermis

in *Diclidanthera laurifolia*. The stomata are found only on the lower surface of the leaf in all the investigated species and are, as a rule, surrounded in an irregular manner by a variable number of epidermal cells; in *Symplocos* alone, a subsidiary cell is placed parallel to the pore on each side of the pair of guard-cells. The latter are either on the same level as the epidermis or project above it, the latter feature being associated with a dense hairy clothing on the lower side of the leaf, as in *Styrax camporum*. The structure of the smaller veins varies, and is of value for specific diagnosis. In *Styrax camporum*, even the smaller veins are provided with sclerenchyma, and are vertically transcurrent above by means of cells with wide lumina; the latter statement also applies to the smaller veins in *Pamphilia styraciflua*. In *Symplocos adenophylla*, on the other hand, the smaller veins, in which the conducting tissue is surrounded by a sclerenchymatous ring, are embedded in the mesophyll. Spicular cells do not occur in the mesophyll (a point of difference from the Ebenaceae); but stone-cells have been observed in the parenchyma of the petiole in *Symplocos adenophylla*. Oxalate of lime is excreted in the form of clustered or solitary crystals along the course of the vascular bundles. Solitary crystals and aggregates, resembling clustered crystals, are found in *Styrax camporum* and *Halesia tetraptera*, clustered crystals in *Symplocos adenophylla* and solitary crystals in special cells, which are sclerosed on the side bordering on the sclerenchyma of the veins, in *Diclidanthera laurifolia*. Large crystal-sacs do not occur in the mesophyll in this Order, which therefore differs from the Ebenaceae in this respect. With regard to the **hairy covering**, it has already been stated above that glandular hairs are wanting, whereas simple, uniseriate hairs, stellate hairs and small scales occur. The simple hairs have a sclerenchymatous wall, which is sometimes finely striated superficially, and a lumen which is septate by means of a few thin division-walls (*Diclidanthera laurifolia*, *Symplocos coccinea*). The stellate hairs have a varying number of rays, and have been observed in the genera *Styrax*, *Pamphilia*, and *Halesia*; their ray-cells, as a rule, have thick walls. The stellate hairs sometimes assume the form of small scales, in consequence of the cells of the ray being united along their entire length or nearly so (*Styrax glabrum*, Sw., *S. glabratum*, Spreng., and *S. leprosum*, Hook. et Arn., according to O. Bachmann).

The **petiole** of *Styrax officinale*, which was examined by Petit, contains a ring of bundles in the characteristic region ('caractéristique').

I have also examined the structure of the **axis** in detail in the above-mentioned five species of the genera *Symplocos*, *Halesia*, *Styrax*, *Pamphilia*, and *Diclidanthera*. The pith presents special features in *Diclidanthera laurifolia*, and in the genus *Halesia*. In the first-named species it contains stone-cells; in *Halesia tetraptera*, L., and *H. diptera*, L., septation of the pith (without sclerosis) occurs, this feature being visible even to the naked eye. The chief characters in the structure of the **wood** may be described as follows. The shape and size of the lumen of the vessels (max. diam. =·036–·07 mm.), the arrangement of the vessels in a transverse section of a branch and the breadth of the medullary rays (1–4-seriate) differ in the individual genera. The perforations of the vessels are scalariform in *Pamphilia*, *Styrax*, *Halesia*, and *Symplocos*; in *Styrax camporum* and *Pamphilia styraciflua* they may have as many as 12 bars, in *Halesia tetraptera* as many as 20, and in *Symplocos adenophylla* a still larger number. Unlike the other genera, *Diclidanthera* has simple perforations only. The vessel-wall, where it is in contact with tissue of the medullary rays, is usually covered with bordered pits, but in *Diclidanthera laurifolia* simple pits accompany the bordered pits in these positions, the former being of the same size as the borders of the latter, while in *Symplocos adenophylla* there are large simple pits and pits arranged in a scalariform manner. The wood-parenchyma is developed to a varying extent; in *Styrax camporum* it contains solitary

crystals. The wood-prosenchyma has rather thick walls without having narrow lumina, and always possesses pits with distinct borders, although sometimes (*Styrax*, *Pamphilia*) the border is smaller than the slit.

The following facts may be mentioned regarding the structure of the **cortex**. The development of cork either takes place superficially, viz. in the epidermis (*Diclidanthera*, with cork composed of stone-cells) or subepidermally (*Symplocos*), whilst in other cases the cork arises in the pericycle internal to the primary hard bast (*Styrax*, *Pamphilia*, *Halesia*, the latter with abundant formation of phelloderm). The pericycle contains isolated groups of bast-fibres in *Styrax*, *Pamphilia*, and *Halesia*, while in *Symplocos adenophylla* the primary groups of hard bast, even in branches such as are met with in herbarium-material, are found to be united to one another by means of branched stone-cells; in *Diclidanthera laurifolia* a composite and continuous sclerenchymatous ring is developed. The primary cortex contains numerous stone-cells in *Diclidanthera laurifolia* and *Symplocos adenophylla*. Sclerenchymatous elements are also present in the secondary bast; thus fibre-like sclerenchymatous cells of the nature of rod-cells, and having abundant pits occur in *Styrax camporum* and *Diclidanthera laurifolia*, true bast-fibres in *Symplocos adenophylla*, groups of cells resembling sclerenchymatous fibres in *Pamphilia styraciflua*, and also, according to Tschirch, in the older branches of *Styrax Benzoin*; these latter elements resemble the well-known *Cinchona*-cells and in transverse section show an angular outline and an exceptionally thick concentrically stratified wall.

NOTE.—Since in the preceding description no mention has been made of any special **secretory organs** as occurring in this Order, the question arises as to what kind of receptacles contain the benzoic resin derived from *Styrax Benzoin*. Wiesner and Tschirch have cleared up this matter. The greater part of the benzoic resin is formed in lysigenous intercellular secretory receptacles; these may be observed in the bast in rather thick branches, their development commencing in the medullary rays. Analogous lysigenous resin-spaces also appear in the wood. According to more recent statements made by Tschirch, this formation of resin appears not to take place in healthy trees, but to be a pathological phenomenon.

Literature: Wiesner, Mikrosk. Untersuch., 1872, p. 90.—Möller, Rindenanat., 1882, pp. 201, 202. —Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. i, 1885, pp. 267, 268.—Solereder, Holzstr., 1885, pp. 169, 170.—O. Bachmann, Schildh., Flora 1886, separate copy, p. 20.—Petit, Pétiole, Act. Soc. Linn. de Bordeaux, t. xliii, 1889, p. 30.—Tschirch, Sekretbeh., Ber. deutsch. bot. Gesellsch. 1888, p. 9 et seq.; see also Ang. Anat., 1889, p. 216, and Sitz.-Ber. naturf. Freunde Berlin, No. 9, 1889, pp. 173–5.—Gürke, in Natürl. Pflanzenfam., iv. Teil, Abt. 1, 1891, pp. 166 and 173.—Loesener, Matépfl., Ber. deutsch. pharm. Gesellsch. 1896, separate copy, p. 31. [Barthélemy, *Styrax officinale*, Montpellier, 1895, 51 pp.]

OLEACEAE.

The Oleaceae are excellently characterized by certain anatomical features, which, when taken together with the opposite exstipulate leaves, make it possible and even easy to recognize a member of this Order in the sterile condition. Thus all the Oleaceae possess peltate hairs of varying size, in which the stalk is unicellular, and the shield is segmented solely by means of vertical walls into a variable number of cells, showing different types of orientation (Fig. 119, *C–E*). An additional character is the excretion of oxalate of lime in the form of small, acicular or prismatic crystals (Fig. 119, *A–B*). The stomata usually have no special subsidiary cells. The following characters should be specially pointed out: the absence of bicollateral structure in the vascular bundles, distinguishing this Order from the allied Orders Loganiaceae, Gentianeae, Apocynaceae and Asclepiadeae, and, furthermore, the absence of laticiferous tubes, distinguishing it from the last two of these Orders. In the structure of the axis the superficial formation of cork and the prevalent occurrence of simple perforations in the vessels are of value for anatomical diagnosis; the pitting of the wood-prosen-

chyma varies. Finally the occurrence of sclerenchymatous fibres or of spicular cells in the mesophyll is very common.

The **structure of the leaf** has been investigated, especially by Vesque and Pirotta, and is bifacial in the species examined. The epidermal cells exhibit a number of variations, which are of value for specific diagnosis. They have either straight or undulated lateral walls and are of various dimensions. In certain species the outer walls of the epidermal cells are distinguished by considerable thickness; the cuticle not uncommonly shows undulated striation. Gelatinization of the epidermis of the leaf has not been observed in any case. Hypoderm is not very commonly found; Vesque mentions it as occurring below the upper epidermis of the leaf of *Noronhia emarginata*, Thouars and *Jasminum azoricum*, and it also occurs in the genus *Linociera* (1–2 layered in *L. compacta*, R. Br. and *L. elegans*, Eichl.). Usually the stomata are only found on the lower surface of the leaf; but in *Ligustrum vulgare* (according to Pirotta) and in *Menodora integrifolia*, Steud. (according to my own observation) they also occur rather abundantly on the upper side and they are likewise found in small numbers on this surface in *Syringa vulgaris* and *S. Varinii* (according to Mer). Special subsidiary cells are very rare. Sometimes (*Myxopyrum smilacifolium*, Bl.) the three or four neighbouring cells present are slightly different from the rest of the epidermal cells, while the Rubiaceous type has been demonstrated in the linear leaves of *Ligustrum Massalongianum* (Vesque). But in most cases the pair of guard-cells is surrounded by a varying number of ordinary epidermal cells. It is also worthy of remark that sometimes, e.g. in *Forestiera porulosa*, large and small stomata occur side by side. Regarding the structure of the veins, Vesque and Pirotta must be referred to, since a uniform type is not present and the variations which occur are only of value for specific diagnosis. The occurrence of sclerenchymatous fibres and spicular cells in the mesophyll is widely distributed in the genera *Linociera, Ligustrum, Noronhia, Notelaea,* and *Olea*, but this feature also is only of importance for specific diagnosis.

The sclerenchymatous elements of the mesophyll are present in almost all species of the genus *Linociera* (exception: *L. picrophloia* [F. v. M.]), and show very varied types of differentiation. In *L. intermedia*, Wight, they are only found here and there in the smaller veins as sclerosed cells of the palisade-tissue; in many species they are developed as sclerenchymatous fibres traversing the mesophyll more or less irregularly (e.g. *L. verrucosa*, Solered.), while in other species (e.g. *L. arborea*, Eichl.) the sclerenchymatous fibres run in the same direction as the palisade-cells. From these it is no great step to the columnar, sclerenchymatous cells of *L. compacta*, R. Br., &c., which are elongated in the same direction as the cells of the palisade-tissue and frequently connect the upper and lower epidermis or terminate in a root-like manner in the mesophyll; these elements also show transitions to the abundantly branched spicular cells of *L. insignis*, Clarke, &c. Certain very peculiar elements are found in *L. glomerata*, Pohl, viz. sac-like cells with wide lumina and rather thick, wrinkled, and transversely folded walls; they extend from one epidermis of the leaf to the other, and are sometimes forked. For details regarding *Linociera*, see Solereder, 1891. Sclerenchymatous fibres traversing the leaf irregularly are also present in varying abundance in certain species of *Olea* (*O. americana, O. angustifolia, O. chrysophylla, O. europaea, O. undulata*), according to Pirotta and Vesque, in *Visiania paniculata* (=*Ligustrum glomeratum*, Bl.), according to Pirotta, and in *Noronhia emarginata*, Thouars, according to my own observation; sclerenchymatous cells of the type found in *Linociera compacta* occur in *Piccona excelsa* (=*Notelaea excelsa*, Webb. et Bert.), *Osmanthus fragrans*, and *O. ilicifolius* (=probably *O. Aquifolium*, S. et Z.), according to Pirotta, and in *Notelaea longifolia*, Vent., according to my own observation; lastly, stone-cells are found in the tissue of the petiole of *Fraxinus juglandifolia* and *Chionanthus fragrans*, according to Pirotta.

Oxalate of lime is only excreted in the form of small acicular crystals or prisms. These often occur in large numbers, filling each cell of the epidermis (e.g. *Forestiera porulosa*, Poir., Fig. 119, *A*) or mesophyll of

the leaf (*Olea europaea*, L., Fig. 119, *B*, *Noronhia emarginata*, Thouars), and also constitute the only form of excretion in the tissues of the axis. Nuclear crystalloids are widely distributed (*Jasminum*, *Forsythia*, *Syringa*, *Fraxinus*, *Ligustrum*) in the cells of the leaf-tissue, according to Zimmermann.

The characteristic form of hair in this Order is that of peltate **trichomes** of variable size, having a unicellular stalk and a shield which is divided by vertical walls only. These peltate hairs are usually glandular [1], and in *Olea* alone have a clothing function; they have been shown to be present [2] in all the genera. The peltate hairs of the species of *Olea* are especially distin-

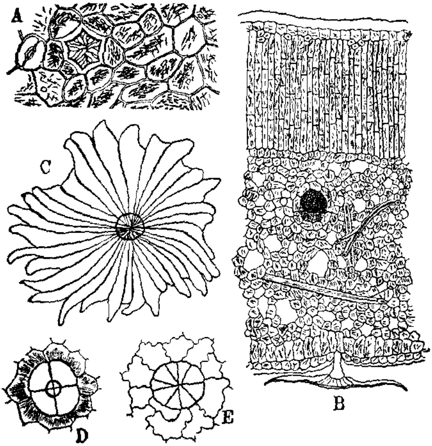

FIG. 119. A, Epidermis of the lower side of the leaf of *Forestiera porulosa*, Poir., showing a depressed gland and the numerous small raphides in the cells. B, Transverse section of the leaf of *Olea europaea*, L. with sclerenchymatous fibres and a peltate hair, and showing extreme abundance of small raphides. C, Peltate hair of *Olea europaea*, L. in surface-view. D, Glandular hair of *Jasminum officinale*, L. E, Glandular hair of *Linociera micrantha*, Mart.—Original.

guished from the 'peltate glands' occurring in the remaining genera, by the size of their shield, which attains a diameter of ·17 mm. The stalk is unicellular, as in the peltate glands; the shield consists of 10–30 cells, which radiate from its centre but become free from the adjoining cells at the margin of the shield, so that the latter acquires a jagged appearance (Fig. 119, *B*–*C*). In young stages the peltate hairs have the same appearance as the peltate glands which will now be described. The peltate glands are essentially distinguished

[1] The glands on the bud-scales of *Syringa* and *Forsythia* have the same structure as the peltate glands, only their stalk is longer and uniseriate (Hanstein).

[2] Peltate hairs have been observed by Prillieux in species of *Jasminum*, *Forsythia*, *Syringa*, *Fraxinus*, *Fontanesia*, *Phillyrea*, *Osmanthus*, *Chionanthus*, *Olea* and *Ligustrum*, by me in *Menodora integrifolia*, Steud., *Nyctanthes arbor tristis*, L., *Schrebera swietenoides*, Roxb., *Forestiera porulosa*, Poir., many species of *Linociera*, *Notelaea longifolia*, Vent., *Noronhia emarginata*, Thouars and *Myxopyrum smilacifolium*, Bl.

from the hairs of the species of *Olea* only by their smaller shield, the diameter of which usually lies between ·045 and ·06 mm., and rarely attains ·08 mm. Owing to their small diameter, the peltate glands appear more like capitate hairs in a transverse section of the leaf and can rarely be seen by the naked eye or with a lens; the latter is possible, for instance, when they give rise to depressed (*Noronhia emarginata*) or even transparent (*Forestiera porulosa*) dots owing to their being sunk in the surface of the leaf. The margin of the shield in these peltate glands is either circular or slightly lobed in consequence of the projection of the component cells, which invariably show a radiate arrangement. The number and mode of arrangement of the cells of the shield vary; sometimes they are not even constant in the same superficial section, but these features are nevertheless of value for systematic purposes within certain limits. The number of cells forming the shield lies between 4 and 24. They either radiate from one point or from a median line, or only a certain number of the ray-cells reach the centre of the shield, so that the radial walls of the shield appear bifurcated in surface-view.

In *Jasminum officinale*, L. (Fig. 119, *D*), *Myxosporum smilacifolium*, *Menodora integrifolia*, and *Nyctanthes arbor tristis* the shield consists of 4 cells, which together form an orthogonal cross; in *Jasminum heterophyllum*, Roxb., it consists of 4–6, in *J. Sambac*, Ait., and other species of *Jasminum*, *Ligustrum vulgare*, L., *L. nepalense*, Wall., and *Syringa vulgaris*, L. of 8, in *Syringa persica*, L. of 16 cells. In the other genera the shield consists, as far as is known, of 12–24 cells.

The peltate hairs sometimes form nests in little pits on the lower surface of the leaf, and in that case give rise to nectaries, which are visible even to the naked eye; they have been investigated by Morini in species of *Ligustrum* and *Syringa*, and also occur in species of *Forestiera*, *Olea*, and *Phillyrea*, according to Delpino.

Accompanying the peltate hairs, simple unicellular or uniseriate trichomes are present in many cases. Of these only the unicellular hairs of *Nyctanthes arbor tristis* need be mentioned; these hairs and their neighbouring cells are strongly silicified, and give rise to the white dots which occur on the upper surface of the leaf and are visible to the naked eye. In the neighbouring cells protuberances of the cell-wall resembling cystoliths are to be found; these are usually distinctly stratified and are similar in position and shape to the analogous structures in the small false scales of the Boragineae, which, however, are encrusted with lime.

The structure of the **petiole** has been examined in species of *Forsythia*, *Fraxinus*, *Jasminum*, *Ligustrum*, *Olea*, *Phillyrea*, and *Syringa*. In *Fraxinus excelsior* the principal system of fibro-vascular tissue consists of a ring of vascular bundles in the characteristic region ('caractéristique'); in all other cases it consists of an arc-shaped vascular bundle. Smaller accessory vascular bundles also occur.

The structure of the **wood** is well known [1]. The medullary rays are 1–4-seriate. The arrangement of the vessels and the size of their lumina (diam. = ·15 mm. in *Fraxinus excelsior*, ·036 mm. in *Olea europaea*) vary. The perforations of the vessels are usually simple; I have observed scalariform perforations with one or more bars in *Forsythia*, *Syringa*, and *Fontanesia*. In the species investigated by me, the walls of the vessels bear bordered pits where they are in contact with parenchyma of the medullary rays. Spiral thickening of the wall has been observed, especially in vessels with

[1] Kohl has investigated 37 species of the genera *Jasminum*, *Forsythia*, *Syringa*, *Fraxinus*, *Fontanesia*, *Phillyrea*, *Osmanthus*, *Chionanthus*, *Linociera*, *Notelaea*, *Olea*, *Ligustrum* and *Myxopyrum*; I have investigated *Jasminum officinale*, L. and *J. tetraphis*, Wight et Gardn., *Nyctanthes arbor tristis*, L., *Forsythia suspensa*, Vahl, *Syringa vulgaris*, L., *Fraxinus excelsior*, L., *Fontanesia Fortunei*, Zucc., *Linociera micrantha*, Mart., *Olea europaea*, L. See also Möller and Pomrencke, loc. cit.

relatively narrow lumina, in species of *Jasminum, Forsythia, Syringa, Fontanesia, Phillyrea, Osmanthus,* and *Ligustrum.* The wood-parenchyma is only developed in small amount. The wood-prosenchyma bears typically bordered pits in *Jasminum, Forsythia, Fontanesia* and *Nyctanthes*; in the remainder of the genera investigated, it must, generally speaking, be described as having simple pits. It may be added that in *Fraxinus* the slit-like pits of the prosenchyma are, in some cases, distinctly bordered and that in many genera which have wood-prosenchyma with simple pits, tracheides occur side by side with the latter (in considerable numbers in *Syringa*). In species of *Jasminum, Forsythia, Syringa,* and *Fontanesia,* the wood-prosenchyma, which in these cases bears bordered pits, is sometimes provided with a spiral band, while the prosenchyma bearing simple pits in species of *Olea* and *Notelaea* is septate by means of fine division-walls.

The following statements on the structure of the **cortex** are based especially on Möller's investigations, which refer to species of *Jasminum, Syringa, Fraxinus, Phillyrea, Olea,* and *Ligustrum.* The epidermis contains sclerosed cells in all the species of *Fraxinus* investigated by J. E. Weiss. The cork arises subepidermally in *Syringa, Fraxinus, Phillyrea, Chionanthus, Olea, Ligustrum,* and in *Forsythia suspensa,* Vahl, whilst it develops in the epidermis in *F. viridissima,* and internally to the 3–4 layers of massive collenchyma belonging to the primary cortex in *Fontanesia Fortunei,* Carr. (Möller, Vesque, Douliot, J. E. Weiss). The cells of the cork are generally distinguished by their large size and by slight flattening; they have walls of varying thickness and are commonly elongated in the radial direction. The primary cortex is generally collenchymatous in its outer portion. In *Olea europaea,* &c., it contains stone-cells; in *Jasminum fruticans* strands of sclerenchymatous fibres are developed in the angles of the stem, whilst the intermediate portions are occupied by assimilatory tissue (Pick). The pericycle contains a composite and continuous sclerenchymatous ring in *Olea, Phillyrea,* and *Linociera*; in *Jasminum, Syringa, Fraxinus,* and *Ligustrum,* isolated groups of bast-fibres are found, and between them a few stone-cells sometimes occur. In the secondary bast, true bast-fibres may be present (*Fraxinus, Syringa*) or absent (*Jasminum, Phillyrea, Olea, Ligustrum*). The groups of secondary bast-fibres in *Fraxinus* and *Syringa* are often accompanied by stone-cells and occasionally give rise to a stratification of the bast. In *Phillyrea, Olea,* and *Ligustrum* rod-cell-sclerenchyma occurs in place of the bast-fibres, all transitions to ordinary stone-cells being found; in *Jasminum* groups of stone-cells only are present.

The **pith**, according to Gris, is homogeneous in *Olea* and *Phillyrea,* heterogeneous in *Chionanthus, Fontanesia, Forsythia, Fraxinus* incl. *Ornus, Ligustrum,* and *Syringa.* Of the last series of genera, in all except *Fraxinus* (excl. *Ornus*) the central portion of the pith is entirely composed of empty cells with rather thin walls and wide lumina, while the peripheral portion consists of active cells with thick walls; in *Forsythia,* however, the pith subsequently becomes hollow, owing to the resorption of the central portion. In *Fraxinus excelsior* and *F. nigra,* the central portion of the pith also contains active cells, this being a point of difference from *F. Ornus.* Septation of the pith without sclerosis has been observed in *Jasminum officinale,* L., and *J. tetraphis,* Wight et Gardn.

The axis shows no anomalous structure, even in the climbing species of *Jasminum.*

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SALVADORACEAE.

This small Order is most nearly related to the Oleaceae. Its members have opposite leaves and commonly more or less distinct stipular structures; the Order also possesses some characteristic anatomical features. Among these the most important are those furnished by the axis, viz.: simple perforations in the vessels; wood-prosenchyma with simple pits; superficial development of cork; and a characteristic, more or less closed strengthening-ring in the pericycle composed of isolated groups of bast-fibres and parenchymatous cells, which are thickened in the form of a U. The hairy covering is extremely scanty. The tendency to the formation of small peltate hairs (Fig. 120, *C–D*) in *Dobera* and *Platymitium* is very noteworthy, since such hairs are very widely distributed in the allied Order Oleaceae. Both clustered and solitary crystals occur, but do not consist of oxalate of lime (Fig. 110, *A–B*). Internal secretory receptacles are wanting. Finally, the occurrence of interxylary soft bast in *Salvadora*, *Dobera*, and *Platymitium* requires special mention.

In the anatomy of the **leaf**, the following points may be cited in accordance with my own investigation of *Dobera Roxburghii*, Planch., *Platymitium loranthifolium*, Warb., *Salvadora persica*, L., and *Azima tetracantha*, Lam. The epidermal cells invariably have a tetragonal or polygonal outline in surface-view. They are remarkably small in *Dobera Roxburghii* and *Platymitium loranthifolium*, whilst on the upper side of the leaf of *Azima tetracantha* they exceed the usual average size. In *Salvadora persica* the epidermis on both sides of the leaf consists locally of two layers; in *Azima tetracantha* a hypoderm with a single layer of large cells is developed on the upper side. Gelatinization of the epidermis of the leaf does not occur. The stomata are found in equal abundance on both sides of the thick and centrically constructed leaves of *Salvadora persica*, *Dobera Roxburghii* and *Platymitium loranthifolium*, but only on the lower side of the bifacial leaf of *Azima tetracantha*. Special subsidiary cells, in this case placed parallel to the pore, really only occur in *Salvadora*. In the remaining genera the pair of guard-cells is usually surrounded by several neighbouring cells, which in *Dobera Roxburghii* alone are distinguished by the thinness of their walls from the rest of the epidermal cells, and it is a mere accident if subsidiary cells placed parallel to the pore occur here and there. The mesophyll, as already stated, is either centric or bifacial in structure. The centric leaves of *Salvadora persica* and *Dobera Roxburghii* have palisade-tissue (with very narrow cells in *Dobera*) on both sides beneath the epidermis, while the middle region is occupied by a dense tissue resembling a pith, and having wide lumina with little or no chlorophyll-contents; in *Salvadora* this tissue is composed of more nearly iso-diametric, in *Dobera Roxburghii* of palisade-like cells. The mesophyll of *Platymitium loranthifolium* consists only of palisade-cells, the lateral

walls of which are folded like a concertina. Groups of enlarged storage-tracheids are found in the mesophyll of *Dobera Roxburghii* and *Platymitium loranthifolium*.

Oxalate of lime appears to be absent. It is true that one finds clustered and sometimes (in the axis) also solitary crystals, which in their shape, their double refraction, and their reaction with sulphuric acid (formation of gypsum), agree with the ordinary excretions of oxalate of lime; they are, however, essentially distinguished by their gradual solubility in water and acetic acid. Rosenvinge also met with the crystalline excretions in question in the living plant, and showed that they sometimes secondarily re-enter into the metabolism. In accordance with what has been said they consist of an organic salt of lime, as to the composition of which nothing further is known. The special shape of the containing-cells, which is adapted to the large clustered crystals, and the cellulose-membrane, which not uncommonly encloses the crystals in the

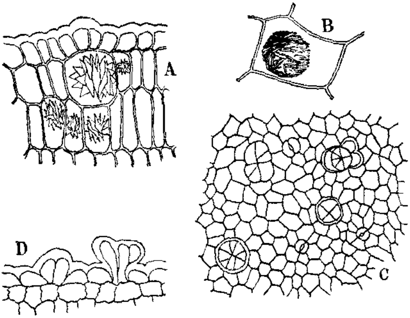

FIG. 120. A, Transverse section through a portion of the leaf of *Dobera Roxburghii*, Planch. with the characteristic clustered crystals (see text); above the large clustered crystal a group of two epidermal cells projects in a papillose manner. B, Smaller clustered crystal from the interior of the leaf of *Salvadora persica*, L. C, D, Epidermis of the leaf of *Platymitium loranthifolium*, Warb. with cell-groups projecting more or less distinctly after the manner of peltate hairs; C, in surface-view; D, in transverse section.—Original.

same way as in the case of Rosanoff's clusters, both support the supposition of the presence of these excretions in the living plant. I have met with these clustered crystals in the mesophyll of the investigated species of all four genera, and in great abundance in *Salvadora persica* and *Dobera Roxburghii*. The clustered crystals of the mesophyll vary in size; the largest assume the form of a star, in which the individual crystals project as long crystalline edges (Fig. 120, *A*); the smaller clusters are more spherical and their individual crystals only project slightly, giving rise to a comb-like contour, so that the surface of the cluster appears as if covered with small acicular crystals without any regular arrangement (Fig. 120, *B*). In addition to the clustered crystals the mesophyll of dried leaves contains numerous fatty bodies.

The **hairy covering**, which is only rarely met with, is formed by unicellular trichomes, the body of the hair consisting entirely of cellulose (branches of *Salvadora oleoides*, Dcne.). The tendency to form small peltate hairs has been observed in *Dobera Roxburghii*, and to a more marked extent in *Platymitium loranthifolium*. In the first-named species (Fig. 120, *A*) groups of four or more epidermal cells become arched outwards to form low papillae on both sides of the

leaf, and appear in surface-view like small Oleaceous peltate hairs, the marginal portions of which are completely fused with the lateral walls of the adjoining epidermal cells. The arching-out of perfectly similar groups of cells on the leaf-surfaces of *Platymitium loranthifolium* (Fig. 120, *C–D*) is much more pronounced and the resulting structure is almost like a hair.

I have examined the structure of the **axis** in *Salvadora paniculata*, Zucc., *S. oleoides*, Dcne., and *S. persica*, L., *Dobera Roxburghii*, Planch., *Platymitium loranthifolium*, Warb., and *Azima tetracantha*, Lam. In the first place the occurrence of islands of soft bast in the wood in *Salvadora* (Rosenvinge), *Dobera* (Radlkofer) and *Platymitium* may be specially pointed out. According to Rosenvinge they are formed by the cambium on its inner side in *Salvadora*, and can be followed right into the wood of the root and through the petiole into the midrib of the leaf. The medullary rays of the wood are rather broad, and 3–5-seriate. The vessels have rounded lumina and attain a maximum diameter of ·036–·05 mm. Their perforations are exclusively simple; their walls have bordered pits, even where they are in contact with parenchyma of the medullary rays. The wood-parenchyma is sometimes (*Salvadora*, *Platymitium*) rather abundantly developed in the neighbourhood of the vessels and of the islands of soft bast. The wood-prosenchyma has thick walls, more or less narrow lumina, and simple pits. The cork is developed subepidermally in *Salvadora* and *Azima*, and consists of cells with wide lumina. The pericycle contains groups of bast-fibres, which are developed in varying amount, and are sometimes elongated in the radial direction; these groups are more or less completely united by cells which are sclerosed in the form of a U (their outer tangential wall remains thin).

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APOCYNACEAE.

1. Review of the Anatomical Features. This natural Order is characterized by a whole series of anatomical features. In the first place, the occurrence of intraxylary soft bast and of laticiferous cells may be mentioned. Further, the lack of glandular hairs (with the exception of glandular shaggy hairs, sometimes appearing on the leaf-base), the superficial origin of the cork, the simple perforations of the vessels, the occurrence of groups of bast-fibres or of isolated bast-fibres in the pericycle of the stem, the almost entire absence of bast-fibres in the secondary bast (except in *Aspidosperma*), and the structure of the bast-fibres (Fig. 122), which will be described more fully in the special portion, are characteristic of the Apocynaceae. The stomata vary; both the Cruciferous and the Rubiaceous types occur. The medullary rays of the wood are narrow; the wood-prosenchyma bears either simple or bordered pits; the vessels usually have bordered pits where they are in contact with parenchyma, but in rare cases there are also simple pits accompanying the former. Oxalate of lime is excreted in the form of ordinary solitary or clustered crystals or styloids. The hairy covering, as a rule, consists of simple, unicellular or uniseriate trichomes. The following anatomical features, which are suitable for special anatomical diagnosis, have been observed: Gelatinization of the spongy tissue (species of *Vahea* and *Clitandra*); hypoderm in the leaf (*Nerium*); formation of papillae on the lower side of the leaf (*Alstonia scholaris*); sclerosed cells in the palisade-tissue (*Aspidosperma Quebracho*, Schlecht.); antler-like trichomes (*Oncinotis*, Fig. 121, *B*); special uniseriate hairs (*Echites*, Fig. 121, *A*); specially shaped sclerenchy-

matous cells in the pith (*Cerbera, Cyrtosiphonia*); secretory cells in the cortex (*Aspidosperma Quebracho, Geissospermum Vellosii*, Peck.); the occurrence of furrows in the xylem-mass of many species, of thin-walled tissue in the xylem-mass (*Echites* sp.), of groups of soft bast situated in the middle of the pith (*Lyonsia straminea*, R. Br., *Mandevillea suaveolens*, Lindl., *Parsonsia heterophylla*, Cunn. and *P. variabilis*, Lindl.), of inversely orientated medullary vascular bundles formed secondarily from the intraxylary phloem (*Apocynum cannabinum*, L. and *Willughbeia firma*, Bl.); finally, the occurrence of islands of soft bast, situated in the wood, which in *Lyonsia straminea*, R. Br. are formed internally by the normal cambium, and in *Condylocarpon*, sp. (Fig. 123) are connected with the formation of furrows in the xylem-mass.

2. STRUCTURE OF THE LEAF. The leaf-structure has been relatively little investigated. Vesque's statements, which are chiefly followed here, are based on the examination of species of the genera *Allamanda, Alstonia, Beaumontia, Carissa, Cerbera* (incl. *Tanghinia*), *Echites, Kopsia, Melodinus, Nerium, Plumeria, Strophanthus, Tabernaemontana, Trachelospermum, Vinca*, and *Wrightia*. The leaf-structure is bifacial in most of the species investigated, but centric in *Nerium Oleander* and *Aspidosperma Quebracho*. The **epidermal cells** on the upper side of the leaf are sometimes of large size (*Allamanda neriifolia, Tabernaemontana, Beaumontia, Cerbera laurifolia*). In *Echitis peltata* and *Alstonia scholaris* the upper epidermis consists locally of two layers; a true hypoderm composed of two or more layers is found in *Nerium Oleander* on both sides of the leaf; this tissue, it may be added, is not of epidermal origin, according to Pfitzer, but belongs to the mesophyll. In *Alstonia scholaris* the lower epidermis shows papillose differentiation. In the **stomata** no uniform type of structure is present. Some members of the Order (species of *Allamanda, Kopsia, Plumeria, Strophanthus, Vinca*; and likewise *Echites peltata*, Vell., according to my own investigation) have stomata, which are accompanied by two or more subsidiary cells parallel to the pore; on the other hand, species of *Cerbera* and *Tabernaemontana* follow the Cruciferous type, having three subsidiary cells. Within the genus *Vinca*, *V. minor* shows the Rubiaceous type, whereas *V. rosea* shows the second type. Finally, in *Melodinus monogynus* both types occur on the same leaf. The stomata usually lie on a level with the epidermis; in *Nerium Oleander* they project strongly, while in *Aspidosperma Quebracho* they are deeply depressed. In the Oleander the stomata show a peculiar grouping; they are found on the lower side of the leaf at the base of deep pits, the entrance to which is occupied by hairs. Special features in the **mesophyll** are the gelatinization of the cell-walls of the spongy tissue, which Radlkofer found to be particularly well developed in *Vahea gummifera*, Lam., *V. crassipes*, Radlk., and *Clitandra cirrhosa*, Radlk., less distinct in *Couma utilis*, J. Müll., and *Hancornia speciosa*, Gomez, and the occurrence of numerous, sclerosed palisade-cells in the leaf of *Aspidosperma Quebracho*. Cork-warts are present in large numbers on the lower side of the leaf in *Pycnobotyra multiflora*, K. Sch. and (according to the description) in *P. nitida*, Benth. also.

According to Petit and Vesque, the **petiole** usually contains a single arc-shaped, bicollateral vascular bundle (*Allamanda, Alstonia, Beaumontia, Cerbera*, &c.); in other cases (*Vinca rosea, Nerium Oleander*) there are also from two to four smaller lateral vascular bundles, which are symmetrically arranged.

The **hairy covering** generally consists of simple, uniseriate (species of *Beaumontia, Echites, Trachelospermum, Wrightia*) or unicellular hairs. The latter are often very small and resemble papillae (upper side of the leaf of the Oleander, species of *Allamanda* and *Vinca*), but sometimes they are longer (lower side of the leaf of *Nerium Oleander, Plumeria alba*). *Vinca rosea* has unicellular and uniseriate trichomes side by side. Special forms of hairs have been observed by me in *Echites peltata*, Vell. (Fig. 121, *A*) and by Radlkofer in

Oncinotis (Fig. 121, *B*). The trichomes of *Echites* are uniseriate; their basal portion, which is sunk in the epidermis, consists of a row of very short, thick-walled cells; the free portion of the hair is composed of cells which have rather thick walls and are firmly united to one another in the lower portion, but have thinner walls and are rounded off in the upper portion. The hairs of *Oncinotis hirta*, Oliv. have the shape of antlers; the main axis and its branches are formed by a row of thick-walled cells. *O. tomentella*, Radlk.[1] has similar hairs, which, however, are smaller and have thinner walls. Glandular trichomes are absent except for glandular shaggy hairs, which have the same structure as in the Rubiaceae, possessing a nucleus of several rows of elongated cells covered by a palisade-like, secretory epidermis; these hairs have hitherto only been met with at the base of the leaf of *Nerium Oleander* (Leonhard).

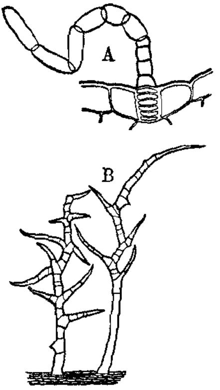

FIG. 121. A, Trichome of *Echites peltata*, Vell. B, Branched hairs of *Oncinotis hirta*, Oliv.—Original.

Oxalate of lime takes the form of clustered crystals, ordinary solitary crystals and styloids. Typical crystal-sand[2] has so far not been observed in the Order by any trustworthy authority. Clustered crystals sometimes (*Oncinotis tomentella*, Radlk.) occupy enlarged cells of the mesophyll. The solitary crystals occasionally occur in the epidermis of the leaf (*Alstonia scholaris* and *Cerbera Manghas*, according to Vesque) and are not uncommonly combined to form peculiar zig-zag figures in the axis (bast of *Cerbera* and *Nerium*). The styloids are found, according to my own observation, in the inner and outer soft bast of *Carissa paucinervia*, DC. and, according to Leonhard, in the axis of *Tabernaemontana laurifolia*, L., and *Cerbera Tanghin*, Hook.

The non-articulated **laticiferous tubes** form one of the two most important anatomical characters and are perhaps quite generally distributed in the Order. In the majority of the species which have been investigated, they are already present in the embryo. According to Chauveaud, their initial cells arise in the plane which coincides with the node of the cotyledons; they here appear in the peripheral part of the central cylinder, and are separated from one another by one or a few cells. Other members of the Order (species of *Vinca*, *Amsonia latifolia*, and *Tabernaemontana Wallichiana*), according to Chauveaud, do not contain laticiferous tubes in the embryo; in these plants the formation of laticiferous elements only takes place subsequently. In the axis of the fully grown plant the laticiferous tubes are found in the pith, in the inner and outer bast, and in the primary cortex; not uncommonly laticiferous tubes penetrate from the cortex through the medullary rays into the pith. In the lamina of the leaf the laticiferous elements generally occur in the veins only. More rarely they

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[1] The statement by A. Weiss (in Karsten, Bot. Untersuch. 1867, p. 381) regarding the occurrence of two-armed hairs in an undetermined species of *Apocynum* is probably due to incorrect determination of the material, since other species of the same genus have conical trichomes only.

[2] Leonhard mentions the occurrence of crystal-sand in *Cerbera Tanghin*, *Carissa* sp. and *Trachelospermum* sp. Possibly this only means the presence of small crystal-grains in the same cell with a solitary crystal, as in *Cerbera laurifolia*, Lodd.

branch off from the latter and run freely in the mesophyll (*Echites peltata*, Vell., according to Trécul and my own observation; *Beaumontia grandiflora, Plumeria acutifolia, P. hypoleuca, Vinca major*, according to Pirotta and Marcatili). In the parenchyma of the petiole also the laticiferous tubes have an irregular arrangement (Vesque). The wall of the laticiferous tubes is generally rather thin, and the lumen not specially wide. Laticiferous tubes with thick walls or wide lumina are rarer (see Leonhard, loc. cit.). The contents of the tubes are sometimes (*Parameria vulneraria*, Radlk.) so much like caoutchouc, that they can be drawn out as threads on breaking a branch. Treub has demonstrated nuclei in them and Trécul has shown that starch-grains occasionally also occur (*Nerium Oleander, Cerbera Manghas*).

Up to the present time no member of the Order has been proved with certainty to be without laticiferous tubes [1]. The erroneous statement in Leonhard's work, that laticiferous tubes are wanting in *Arduina bispinosa*, has been disposed of by demonstration of the fact that the plant investigated by Leonhard was a member of the Rubiaceae, whilst *Arduina bispinosa* possesses the elements in question. Two further exceptions mentioned by Möller, viz. the Quebracho-bark, derived from *Aspidosperma Quebracho*, Schlecht., and specimens of the bark of *Geissospermum Vellosii*, Peck., however require discussion. Even at the outset, these barks cannot be recognized as exceptions, since, according to De Bary, the laticiferous tubes are sometimes (*Asclepias curassavica, Vinca*) wanting in the secondary bast. With regard to the first exception I have found on examination of herbarium material that the laticiferous elements of *Aspidosperma Quebracho* are only developed in the outermost portion of the bast, between the primary groups of hard bast, and are thus really present. Owing to lack of material I could not deal with the second exception; but at present it is not improbable that one may be able to demonstrate laticiferous tubes in the branches of this plant. I may also mention that, according to my own observation, numerous isodiametric secretory cells occur in the bast of *Aspidosperma Quebracho* (branches and druggist's bark); according to Möller, this is also the case in *Geissospermum Vellosii*, Peck., where the cells are short and spindle-shaped.

3. STRUCTURE OF THE AXIS. **Intraxylary phloem** [1] probably occurs in all the members of the Order; at any rate, no exception is known. It either forms a continuous ring or isolated bundles at the margin of the pith. In many cases it increases in thickness by means of a cambium at its outer margin; in some species (*Willughbeia firma*, Bl., and *Apocynum cannabinum*, L., according to Scott and Brebner) this cambium gives off woody tissue externally, so that inversely orientated medullary vascular bundles are formed in the thicker branches. In addition to those at the margin of the pith, bundles of soft bast also appear in the pith itself in some species (*Lyonsia straminea*, R. Br. in the form of two arcs, and, according to Leonhard, in *Mandevilla suaveolens*, Lindl., *Parsonsia heterophylla*, Cunn., and *P. variabilis*, Lindl.).

In the **pith** sclerosis is a frequent phenomenon. The sclerosed elements are either ordinary stone-cells or sclerenchymatous rod-cells, elongated in the vertical direction (the latter, according to Leonhard, in species of *Acokanthera, Alstonia, Carissa, Echites, Landolphia*, and *Tabernaemontana*). Special

[1] The occurrence of laticiferous tubes and of intraxylary phloem has by no means been examined in all the genera. It is therefore advisable to enumerate the investigated genera below (in the serial order of Durand's Index): *Allamanda, Willughbeia, Landolphia, Hancornia, Melodinus, Carissa* (*Arduina*), *Acokanthera, Rauwolfia* (*Cyrtosiphonia*), *Alyxia, Thevetia, Cerbera* (*Tanghinia*), *Kopsia, Aspidosperma, Amsonia, Vinca, Plumeria, Alstonia, Tabernaemontana, Thenardia, Forsteronia, Lyonsia, Parsonsia, Wrightia, Nerium, Strophanthus, Parameria, Urceola, Apocynum, Ichnocarpus, Baissea* (*Cleghornia*), *Rhynchodia, Trachelospermum, Beaumontia, Echites, Dipladenia, Mandevilla*. Chimani mentions 'segmentation of the laticiferous tubes' in *Willughbeia javanica*, which sounds improbable for a member of this Order. The intraxylary phloem also appears in the roots of *Vinca major* and *V. media*, which possess pith, but not in those of *V. minor*, where the pith becomes sclerosed at an early stage.

sclerenchymatous elements found in the pith are the branched sclerenchymatous cells of *Carissa Arduina* (Gris) and those of *Cerbera lactaria*, Buch.-Ham., and *Cyrtosiphonia spectabilis*, Miq., which have thick walls and narrow lumina, sometimes attain a length of 2 mm., are attenuated at the ends and sometimes branched; these cells have a curiously verrucose surface (Leonhard).

FIG. 122. Portion of a cell (about twenty years old) from the hard bast of *Nerium Oleander*, L. (very highly magnified) with a local enlargement; around the protoplasm in this enlargement new cell-membranes, described as caps of cell-wall, have been formed; the transverse striation is indicated on those parts of the fibre which have retained the normal size.—After Krabbe.

Regarding the structure of the **wood**, the following facts require mention. The medullary rays are generally narrow, at any rate in branches from herbarium-material, while they are broader (as much as 7 cells thick) in the wood of the trunk. No general statements can be made with regard to the arrangement, size of lumen, and abundance of the vessels; in the lianes the lumen of the vessels often attains considerable dimensions in the later-formed, secondary wood. The perforations of the vessels are simple[1] in the species of the genera *Carissa, Allamanda, Rauwolfia, Echites,* and *Forsteronia,* examined by me. In the same species the walls of the vessels bear only bordered pits where they are in contact with parenchyma of the medullary rays; in *Plumeria acutifolia*, Poir., simple pitting is also present, according to Pomrencke. Spiral thickening of the vessel-wall is mentioned by Leonhard and Möller as occurring in species of *Vinca, Carissa,* and *Tabernaemontana*; scalariform bordered pitting is described by Leonhard in *Plumeria rubra*, L. The wood-parenchyma may be scanty or developed in moderate abundance (e.g. in *Allamanda oenotheraefolia*, Pohl). The wood-prosenchyma bears bordered pits in the species examined by me, although in varied abundance and with borders which vary in size; according to Leonhard and Pomrencke, prosenchyma with simple pits also occurs in the Order.

In describing the structure of the **cortex**, the first place should be given to the development of the cork. This tissue is always formed superficially in the numerous cases investigated, either in the epidermis[2] or subepidermally[3] (Vesque, Douliot, Leonhard). Within these limits the point of origin of the cork may differ in different species of the same genus. The periderm, according to Möller, either consists of very wide cells with thin walls (e.g. in *Nerium Oleander*, L.) or is stratified into several layers, some of which have their cells sclerosed on all sides (e.g. in *Geissospermum Vellosii*, Peck.); in other cases again it is composed of only a few rows of cork-cells slightly sclerosed on one side and of more massive layers of cubical or flat cork-cells (e.g. in *Aspidosperma Quebracho*). Formation of phelloderm is not rare. The pericycle contains bast-fibres, which are either isolated or united into groups; these fibres are generally distinguished by their white colour and their stratification, and often show the 'spiral striation,' 'transverse lamellation,' and 'constriction,' which have been described in detail by Krabbe. We cannot here deal with more than the last of these features, which, however, is sometimes only to be seen in branches of several years' growth. In their longitudinal course, the fibres (Fig. 122) appear constricted at intervals to a small diameter and then suddenly much enlarged. This is a case of local secondary enlargement of the bast-fibres

[1] I do not know what Leonhard means by the term 'doppelte Perforationen.'

[2] This applies to species of *Alyxia, Apocynum, Carissa, Cerbera, Kopsia, Landolphia, Mandevilla, Nerium, Plumeria, Parsonsia, Strophanthus, Tabernaemontana, Thenardia, Vinca.*

[3] This applies to species of *Allamanda, Alstonia, Alyxia, Beaumontia, Cerbera, Cyrtosiphonium, Echites, Lyonsia, Plumeria, Rauwolfia, Tanghinia, Thevetia, Trachelospermum, Vinca.*

accompanied by an encystment of the protoplasm in the widened portion of the fibre by means of the formation of caps of cellulose [1]. In the secondary phloem bast-fibres have only been observed in the Quebracho-bark, where they are accompanied by chambered crystal-fibres with fine, large, solitary crystals. Stone-cells have been met with in certain species in the bast, as well as in the primary cortex.

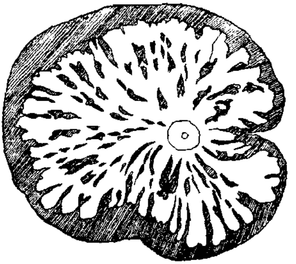
FIG. 123. Transverse section of the stem of *Condylocarpum* sp.; the cortex and the internal bast-tissues are shaded, the pith and periaxial wood are indicated by circular lines.—After Fritz Müller.

Since most of the Apocynaceae are lianes, **anomalies in the structure of their axis** may be expected at the outset. Many Apocynaceous lianes, however, e. g. *Forestiera brasiliensis*, A. DC., have normal structure. The anomaly of a furrowed xylem-mass is widely distributed in the Order; the furrows are occupied by soft bast and the cambium extends between wood and bast throughout the furrow (*Condylocarpon Rauwolfiae*, Müll. Arg., according to H. Schenck; *Echites* sp., according to Jussieu; *Allamanda Hendersoni*, *Lyonsia straminea*, R. Br., *Parsonsia heterophylla*, Cunn., and *P. variabilis*, Lindl., *Tabernaemontana laurifolia*, L., as well as *Alstonia* sp. and *A. scholaris*, R. Br.[2], according to Leonhard). A second anomaly, connected with that of the furrowed xylem-mass, is shown by a stem of *Condylocarpum* sp. from the neighbourhood of Desterro (Fig. 123); this was figured by Fritz Müller and is 7·5 cm. in thickness. The young stem shows furrow-formation; subsequently the furrows become covered in by the further growth of the wood, and new furrows originate at the margin of the latter, but soon undergo the same fate. Thus the transverse section of an older stem shows numerous islands of phloem scattered irregularly in the wood and elongated in a radial direction. The third anomaly found in the Order is the occurrence of interxylary phloem in *Lyonsia straminea*, R. Br. The islands of soft bast are here very irregular in shape, contain sieve-tubes with wide lumina, and are given off on the inner side by the cambium, according to my own observation. It may be added that sometimes (*Echites* sp., according to Leonhard) rather large groups of unlignified tissue occur in the secondary wood.

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[1] Suitable objects for observing this feature are, for example, *Nerium Oleander*, *Marsdenia erecta*, *Asclepias Cornuti* and others (Krabbe). In *Aspidosperma Quebracho* I found a stone-cell and crystal-cells enclosed in such an enlargement of the bast-fibres.

[2] K. Schumann rightly questions the correctness of the statement as regards *Alstonia*, since this genus has no species which are lianes.

pp. 30 and 44.—Pirotta e Marcatili, Rapp. tra i vasi laticif. ed il sist. assim., Ann. R. Istit. bot. di Roma 1886, n. 2; abstr. in Just 1886, i, pp. 921, 922.—Krabbe, Strukt. u. Wachst. vegetab. Zellh., Pringsheim Jahrb., Bd. xviii, 1887, pp. 346–421 and Tab. xi–xv.—Petit, Pétiole, Mém. Soc. sc. phys. et nat. de Bordeaux, sér. 3, t. iii, 1887, pp. 361–3 and pl. vi.—Kerner, Pflanzenleben, Bd. i, 1887, pp. 273 and 285.—[Saldanha, Part. anat. de l'*Echites peltata*, Compt. rend. Soc. roy. de bot. de Belgique 1887, pp. 62, 63; abstr. in Just 1887, ii, p. 666 incomplete.]—[Garcin, Rech. sur les A., Ann. Soc. bot. de Lyon, Année xv, 1888, pp. 197–448, 2 pl.; abstr. in Bot. Centralbl. and in Just insufficient.]—Douliot, in Ann. sc. nat., sér. 7, t. x, 1889, p. 378.—Leonhard, Anat. d. A., Bot. Centralbl. 1891, i, pp. 1, 33 et seq. and Tab. i, ii, and correction hereof, loc. cit. 1891, iii, p. 94; the bad editing of this paper made it impossible to take it sufficiently into account, see e. g. the chapter on crystals, p. 130, and the description of the anomalous structure of the branch of *Lyonsia*, p. 66 etc.—Chauveaud, in Ann. sc. nat., sér. 7, t. xiv, 1891, pp. 98–112 and pl. 7.—Hérail, in Compt. rend. 1891, 13 avril.—Scott and Brebner, in Ann. of bot., vol. v, 1891, pp. 283–6 and pl. xix.—Pomrencke, in Arb. bot. Gart. Breslau, 1892, pp. 52–5.—Planchon, Matière médicale, fam. des A., Montpellier, 1894, 364 pp.—H. Schenck, Anat. d. Lianen, 1893, pp. 202–4.—Herbst, Markstr., Bot. Centralbl. 1894, i, p. 356.—Chimani, Milchr., Diss., Bern, 1895 and Bot. Centralbl. 1895, i.—K. Schumann, in Natürl. Pflanzenfam., iv. Teil, Abt. 2, 1895, p. 111.—Grevillius, in Engler, Bot. Jahrb., Bd. xxiii, 1896, p. 77.—Kuhla, Phelloderm, Bot. Centralbl. 1897, iii, p. 227.

ASCLEPIADEAE.

1. Review of the Anatomical Features. The Asclepiadeae, in correspondence with their close relationship to the Apocynaceae, have the same ordinal anatomical characters as the latter, viz.: bicollateral vascular bundles, laticiferous cells, superficial development of the cork, a rather broad ring of pericycle in the branch containing isolated groups of bast-fibres or solitary bast-fibres, absence of bast-fibres in the secondary bast, simple perforations in the vessels and narrow medullary rays in the wood. The vessels have bordered pitting on their walls, even where they are in contact with parenchyma. The wood-prosenchyma has varied structure, bearing either simple or bordered pits. In like manner various types of stoma occur; the Rubiaceous type, however, is the one most widely distributed. Oxalate of lime is excreted in the form of clustered and solitary crystals. The hairy covering consists of simple and usually uniseriate, more rarely unicellular hairs; in *Dischidia* unicellular trichomes with a glandular function, as well as glandular shaggy hairs have been observed. Of special anatomical features the following may be mentioned: formation of hypoderm in the leaf (species of *Hoya* and *Tylophora*); sclerenchymatous fibres and laticiferous tubes, running irregularly in the mesophyll (*Dischidia Rafflesiana*, Wall.); special hemitropic crystals of oxalate of lime (in some Periploceae); occurrence of groups of soft bast in the pith (species of *Ceropegia*, *Kanahia*, and *Stephanotis*), of sclerenchymatous fibres in the pith (species of *Cryptolepis* and *Cryptostegia*) and of sclerenchymatous fibres in the primary cortex (*Sarcostemma viminale*, R. Br.). The following anomalies in the structure of the branch occur: Irregularities in the secondary growth of the wood in many climbing species, a furrowed xylem-mass (*Gymnema sylvestre*), islands of soft bast in the wood (*Asclepias obtusifolia*, Michx. and '*Ceropegia macrocarpa*'), and thin-walled tissue in the xylem-mass (species of *Gonolobus* and *Ceropegia*).

2. Structure of the Leaf. This has been investigated in only a few species, and principally by Vesque. The leaf-structure is centric in the fleshy leaves of *Ceropegia Sandersoni* and *Hoya carnosa*, as well as in the membranous leaves of *Marsdenia erecta*, but is bifacial in many cases. The epidermis in xerophilous species shows adaptations corresponding with their habit, such as considerable thickness of the cuticle (*Ceropegia stapeliaeformis*, *Hoya carnosa*), excretion of wax on the surface (*Stapelia*), enlargement of the cells on the upper side of the leaf and development of hypoderm (*Hoya carnosa*, *Tylophora laevigata*[1]). The stomatal apparatus usually belongs to the Rubia-

[1] Gelatinization of the epidermis of the leaf has not been observed in the Order. The strong thickening of the outer walls of the epidermal cells in *Solenostemma Argel*, Hayne, described a

ceous type (species of *Asclepias*, *Ceropegia*, *Cryptostegia*, *Hoya*, *Marsdenia*, *Periploca*, *Tylophora*). In *Ceropegia stapeliaeformis* secondary division-walls appear in the subsidiary cells, which are parallel to the pore. The stomata of *Stapelia* (Vesque [1]) and *Hoya bella* (Benecke) have three subsidiary cells as in the Cruciferous type. Sclerenchymatous fibres, running irregularly in the mesophyll, are found in *Dischidia Rafflesiana*, Wall., both in the ordinary and in the ascidiform leaves.

Oxalate of lime occurs in the form of solitary or clustered crystals in the axis and leaf. According to Vesque and Treiber, crystals of a special shape are found in the phloem of some Periploceae (species of *Periploca*, e.g. *P. graeca*, *Cryptolepis* and *Cryptostegia*). They consist of a central portion, which is composed of two truncated pyramids, joined together by their basal surfaces, and externally of two other truncated pyramids, having their truncate (smaller) surfaces in connexion with the central pyramids, while their (larger) basal surfaces are directed outwards. Phosphate of lime is deposited in the form of sphaero-crystals in alcohol-material of *Stapelia* and *Ceropegia* (Kohl). The **laticiferous cells** have the same course of development and structure [2], the same general occurrence [3], and the same distribution in leaf and axis as in the Apocynaceae. Laticiferous tubes, running freely in the mesophyll, have been found in *Araujia sericifera*, Brot. (Trécul), *Daemia tomentosa*, Vatke (Volkens), *Asclepias curassavica* (Groom, Haberlandt), and in *Dischidia* (Scott and Sargant).

Usually the **hairy covering** only consists of unicellular or uniseriate clothing hairs, both of which may sometimes (*Araujia sericifera*) occur side by side in the same species. In *Dischidia*, Scott and Sargant mention the occurrence of hemispherical unicellular hairs, which have a glandular function, excrete mucilage beneath the cuticle, and are present in abundance on both forms of leaf, as well as of mucilage-excreting shaggy hairs, which either only form conical cellular prominences on the surface of the leaf and petiole, or project as ellipsoidal trichomes, having the same structure as the glandular shaggy hairs of *Nerium* and the Rubiaceae. Hanstein observed the same type of glandular shaggy hairs in the leaf-axils of *Asclepias*.

According to Vesque and Petit, the **petiole** contains a single, bicollateral, and arc-shaped vascular bundle, sometimes accompanied by a small vascular bundle at each end.

The structure of the **ascidiform leaves** of *Dischidia Rafflesiana*, to quote the results of Scott and Sargant, confirms the view arrived at by Treub through a developmental investigation, viz. that the ascidia are leaves which owe their origin to extreme intercalary growth in the entire region between the apex and petiole, the upper side of the leaf being that which is more especially affected by this growth. In correspondence with this, more stomata are found on the inner side of the ascidium (the morphologically lower side) than on the outer side (the morphologically upper side); the differentiation of the mesophyll and the orientation of the wood- and bast-portions of the veins also agree with this view.

3. STRUCTURE OF THE AXIS. The structure of the axis is well known through the work of Treiber.

Like the very closely related Apocynaceae, the Asclepiadeae [4] possess

mucilage by Tschirch and Oesterle (Atlas, Taf. vii) and by Walliczek (in Pringsheim Jahrb., Bd. xxv, p. 236), does not show the reactions of mucilaginous membranes.

[1] Jakó, contrary to Vesque's statements, describes a stomatal apparatus in *Stapelia* resembling the well-known *Tradescantia*-type.

[2] The supposed septation of the laticiferous tubes mentioned by Möller as occurring in the bast of *Gonolobus Condurango*, is probably referable to incorrect interpretation or observation.

[3] Possibly laticiferous tubes may be wanting in some cases, e.g. in *Pergularia*, which requires further investigation. See the following note.

[4] As by no means all the Asclepiadeae have been investigated with regard to the presence of intraxylary soft bast and laticiferous tubes, an enumeration of the genera examined may follow here:

intraxylary phloem, which is developed in the form of cell-groups or as a continuous ring at the margin of the pith. An increase of this phloem takes place either by a cambium appearing at its outer margin (e.g. in *Periploca graeca*, L.), or by simple divisions in the phloem itself (e.g. in *Hoya imperialis*, Lindl.), or by both methods in the same species. In rare cases (*Periploca graeca*, according to Scott and Brebner) the cambium also produces a few xylem-elements externally. The internal soft bast is in many cases (species of *Calotropis, Gomphocarpus, Periploca*, &c.) supported at its inner margin by bast-fibres, which sometimes (*Periploca graeca*) only appear relatively late. Groups of soft bast have been met with in the inner portion of the pith in *Ceropegia stapeliaeformis*, Haw., *Kanahia laniflora*, R. Br., and *Stephanotis floribunda*, A. Brongn.

As regards the structure of the **wood**[1] the same features are found in the Asclepiadeae as in the Apocynaceae, viz.: vessels with very wide lumina in the lianes; vessels with simple perforations and with bordered pitting, even where they are in contact with parenchyma; narrow medullary rays, the cells of which are elongated in the vertical direction; wood-prosenchyma generally having bordered pits, sometimes (*Sarcostemma*, according to Treiber) also simple pits.

The most noteworthy features in the structure of the **cortex** are, as in the Apocynaceae, the superficial development of the cork, a rather broad pericycle with isolated groups of bast-fibres or solitary bast-fibres, and the lack of these elements in the secondary bast. The cork develops either in the epidermis[2] or subepidermally[3] (Möller, Vesque, and Treiber). The cork-cells are tabular and mostly thin-walled; in rare cases (e.g. *Periploca graeca* or *Cynanchum Schimperi*, Hochst.) they are strongly thickened. Formation of phelloderm occurs. The primary bast-fibres commonly have the same secondary enlargements, the same striation and transverse lamellation, as in the Apocynaceae.

The following statements may be added regarding the structure of the cortex. The primary cortex contains collenchyma in varying amount, and, in certain species, assimilatory parenchyma resembling spongy or palisade-tissue is present. Stone-cells are not rare in the primary cortex, and sometimes (*Hoya carnosa*, R. Br.) form a ring. Sclerenchymatous fibres have been met with in the primary cortex of *Sarcostemma viminale*, R. Br. Peculiar knob-like structures on the pit-membranes of the primary cortical parenchyma, and in some cases also small rod-like bodies in the intercellular spaces of the same tissue, were first demonstrated by Borscow in *Ceropegia aphylla* and afterwards by Treiber in *Ceropegia Sandersoni*, Decne., and *Cynoctonum angustifolium*, Decne.; according to Treiber they consist of a substance resembling gum or mucilage, and are similar to the structures described by Schenck in the intercellular spaces of the parenchyma of the Marattiaceae. It remains to mention that the primary cortex is usually delimited from the pericycle by an endodermis, and that a ring of stone-cells sometimes (*Leptadenia abyssinica*, Decne., *Periploca laevigata*, Ait., *Sarcostemma viminale*, R. Br.) appears internally to the pericycle.

As regards the structure of the **pith**, we may mention the occurrence of large intercellular spaces in *Periploca graeca*, L., species of *Araujia* and *Gomphocarpus*, of stone-cells in *Astephanus linearis*, R. Br., *Hoya carnosa*,

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Cryptolepis, Cryptostegia, Tacazzea, Periploca, Secamone, Toxocarpus, Microloma, Astephanus, Araujia, Oxypetalum, Xysmalobium, Gomphocarpus, Calotropis, Asclepias, Enslenia, Kanahia, Cynanchum, Sarcostemma, Daemia, Eustegia, Gonolobus, Gymnema, Tylophora, Marsdenia, Stephanotis, Hoya, Dischidia, Leptadenia, Ceropegia and *Stapelia.*

[1] I have examined species of *Periploca, Cryptolepis, Secamone, Toxocarpus, Daemia, Gonolobus, Marsdenia, Gymnema, Leptadenia.* See also Treiber, loc. cit.

[2] In species of *Asclepias, Ceropegia, Cryptolepis, Cynoctonum, Gomphocarpus, Gonolobus, Periploca.*

[3] In species of *Cryptostegia, Cynanchum, Dischidia, Hoya, Periploca, Stephanotis, Tacazzea.*

R. Br., and other species of *Hoya*; and of sclerenchymatous fibres in *Cryptolepis longiflora*, Hort. Berol., and *Cryptostegia longiflora*, Hort. Berol.

Anomalous structures in the axis are known in a number of species. In many cases the anomaly is limited to a specially strong development of the secondary wood and abundant development of vessels at two or four points. In those cases in which the increase of the xylem-mass is greater on two opposite sides, a displacement of the elliptical figure of the transverse section of the stem through a right angle is always found on comparing two successive internodes; in like manner the long axis of the pith is simultaneously displaced, if the latter has an elliptical transverse section, its long axis being always placed at right angles to the long axis of the elliptical section of the stem. These features are described by Hérail in *Ceropegia Sandersoni*, by Witte in *Ibatia muricata*, and by Treiber in a whole series of climbing species. A furrowed xylem-mass is mentioned in *Gymnema sylvestre* by Jussieu, and a well-marked cleavage of the wood in *Calotropis* by K. Schumann. In the xylem-mass of *Gonolobus Condurango*, Tr., '*Ceropegia macrocarpa*' and *Ceropegia Sandersoni*, Decne., larger or smaller areas of unlignified tissue have been noticed. In two species islands of soft bast have been observed in the wood, viz. in the plant described as '*Ceropegia macrocarpa*' and in *Asclepias obtusifolia*, Michx. In the former they originate subsequently by the differentiation of cell-groups in the unlignified portions of the xylem-mass (Treiber). In *Asclepias obtusifolia*, which was examined by Scott and Brebner, the interxylary phloem is only developed in the basal portion of the stem and in the root. The islands of soft bast in the wood of the root are in some cases continuations of the intraxylary phloem of the stem, in other cases they are phloem-islands given off internally by the cambium; others again are due to bundles of sieve-tubes formed secondarily in the thin-walled parenchyma which belongs to the wood of the root and increases by a process of dilatation.

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LOGANIACEAE.

1. Review of the Anatomical Features. In the subsequent description I shall follow my revision of the Loganiaceae in the 'Natürliche Pflanzenfamilien' as regards the delimitation and subdivision of the Order. The classification [1] which I established differs essentially from that in Bentham and Hooker's 'Genera Plantarum,' and is the result of an exomorphic and endomorphic investigation. Of the thirty-four genera enumerated in Durand's Index, the three, *Gaertnera*, *Pagamea* and *Hymenocnemis*, should be excluded from the Order and transferred to the Rubiaceae; the two genera *Desfontainea* and *Plocosperma* may be appended to the remaining genera of the Loganiaceae as *genera dubia*, until a correct place in the system can be assigned to them. Not only the limits, but also the subdivision of the Order, are essentially different in my revision from what they are in Bentham and Hooker's work. And in this respect the anatomical features proved to be of special value. With the help of these characters the genera may be divided into two large groups: the Loganioideae, which are distinguished by the possession of intraxylary soft bast, the absence of glandular hairs (with the exception of the glandular shaggy hairs, occurring at the lower limit of the leaf-base in some genera), and the superficial development of the cork; and the Buddleioideae, in which intraxylary soft bast is wanting, while glandular hairs are present (with a peltate, flattened head, which is bicellular or multicellular owing to the formation of vertical walls), and the cork, as a rule (with the exception of *Polypremum* and *Peltanthera*, both of which have superficial cork-formation), originates in the pericycle.

Apart from the above-mentioned anatomical features, which are so important for the subdivision of the Order, it may be pointed out that in all cases the vessels of the wood have chiefly simple perforations (with the exception of species of the genera *Geniostoma*, *Labordia*, and *Mitreola*, in which scalariform perforations accompany those of the simple type, though in smaller numbers), and, where the vessels are in contact with parenchyma of the medullary rays, they usually have bordered pits only, rarely (in species of *Fagraea*, *Gomphostigma*, *Buddleia*) accompanied by simple pits; in the cortex a composite and continuous sclerenchymatous ring is never present on the outer side of the bast; special, internal secretory organs, such as laticiferous tubes, &c., are completely absent. The type of stoma is not uniform; in the two genera *Gelsemium* and *Strychnos* the stomata are accompanied by subsidiary cells placed parallel to the pore; in many Loganiaceae the stomata are surrounded by three, in others by a larger number of epidermal cells. Oxalate of lime is excreted in the form of ordinary solitary or clustered crystals, small crystals of various shapes, often acicular crystals (in many cases, especially the members of the Buddleioideae), typical crystal-sand (*Couthovia*), styloids (*Bonyunia*, *Usteria*) or styloid-like crystals (species of *Strychnos*).

The following special features may be used for more restricted diagnosis: the occurrence of a mucilaginous layer beneath the upper epidermis of the leaf (species of *Coinochlamys*, *Mostuea*, *Logania*, and *Mitrasacme*) and of mucilaginous cells in the mesophyll (species of *Geniostoma* and *Mitrasacme*); the formation of papillae on the lower epidermis of the leaf (species of *Strychnos*

[1] Review of the new classification: I. Loganioideae: 1. Gelsemieae: *Gelsemium*, *Coinochlamys*, *Mostuea*; 2. Loganieae: *Logania*, *Geniostoma*, *Labordia*; 3. Spigelieae: *Spigelia*, *Mitreola*, *Mitrasacme*; 4. Antonieae: *Usteria*, *Bonyunia*, *Antonia*, *Norrisia*; 5. Strychneae: *Strychnos*, *Gardneria*, *Couthovia*; 6. Fagraeeae: *Fagraea*, *Potalia*, *Anthocleista*. II. Buddleioideae: *Polypremum*, *Peltanthera*, *Nuxia*, *Gomphostigma*, *Chilianthus*, *Emorya*, *Buddleia*, *Adenoplea*, *Adenoplusia*, *Nicodemia*. III. Genera dubia: *Plocosperma* and *Desfontainea*.

ıd *Logania*); the development of hypoderm in the leaf (species of *Geniostoma, abordia, Bonyunia, Antonia, Norrisia, Couthovia, Fagraea, Anthocleista, eltanthera,* and *Nuxia*); cork-warts on the lower side of the leaf (species of *nthocleista* and *Fagraea*); branched spicular cells in the parenchyma of the af, pith and primary cortex (species of *Fagraea, Anthocleista, Potalia*; also ı the tissue of the leaf in species of *Strychnos*); the varied structure of the xternal glands in the Buddleioideae, the peltate terminal portion being 4-celled ı *Polypremum*, while in *Nuxia* it is sometimes 2–4-celled, sometimes many-celled, s is also the case in *Peltanthera*, although in all three genera it has a circular utline, whereas in the other genera of the Buddleioideae it is always 2-celled Fig. 124, *A*), but varies in the shape of its contour; the occurrence of characeristic, four-rayed stellate hairs, of small scales (species of *Chilianthus, Gomhostigma,* and *Buddleia*), or of candelabra-hairs (species of *Chilianthus* and *Buddleia*), both the terminal portions and the tiers of which consist of only two ells (Fig. 124, *B–E*); the occurrence of wood-prosenchyma bearing bordered or simple pits (differing in the different genera); the occurrence of lamellated cork (characteristic of *Geniostoma, Labordia,* and *Couthovia*, see Fig. 125); the development of a ring of stone-cells in many species of *Strychnos*, either in the middle of the primary cortex or in the outermost portion of the bast; the appearance of islands of soft bast in the wood in species of the genera *Strychnos, Antonia, Norrisia, Bonyunia,* and *Logania*, of medullary groups of soft bast (*Antonia* and *Norrisia*), and of cortical vascular bundles having concentric structure (*Anthocleista*).

2. Structure of the Leaf. The leaf-structure is bifacial in most cases. Centric structure of the mesophyll rarely occurs (*Logania linifolia*, Schlecht., *Nuxia floribunda*, Benth., *Gomphostigma scoparioides*, Turcz., numerous species of *Strychnos*). The **epidermal cells** have straight or undulated lateral walls. In certain species of *Coinochlamys* (*C. angolana*, Moore), *Mostuea* (*M. Brunonis*, Dietr.), *Logania* (*L. serpyllifolia*, R. Br., and *L. campanulata*, R. Br.) and *Mitrasacme* (*M. canescens*, R. Br., *M. capillaris*, Wall., *M. divergens*, Hook. f., *M. nudicaulis*, Reinw., *M. polymorpha*, R. Br., *M. serpyllifolia*, R. Br.) a massive mucilaginous layer occurs beneath the epidermis on the upper side of the leaf. A developmental investigation is necessary to determine whether this layer arises, as one may assume to be the case, by gelatinization of the inner walls of the upper epidermal cells. I have not met with isolated epidermal cells having mucilaginous internal walls in any member of the Order; on the other hand, cells with partially gelatinized walls are present in the spongy tissue of *Mitrasacme canescens, M. nudicaulis, M. pilosa*, Labill., *M. polymorpha, M. serpyllifolia*, and *Geniostoma angustifolium*, Bout. In *Buddleia americana*, L., and *Adenoplea sinuata*, Radlk., the outer walls of the epidermal cells on the upper side of the leaf are arched outwards in sub-papillose form; the development of papillae on the lower epidermis is likewise rare and has only been observed in some species of *Logania* (*L. angustifolia*, Sieb., *L. floribunda*, R. Br., and *L. revoluta*, R. Br.), as well as in *Strychnos lucida*, R. Br., which is easily distinguished by this character from the very closely related *S. nux vomica*, L. In certain species of *Strychnos* the epidermal cells are sometimes divided by thin vertical walls, or in places by horizontal walls as well. The latter feature leads up to the occurrence of **hypoderm**, which has been demonstrated in certain species[1] of *Geniostoma, Labordia, Bonyunia, Antonia, Norrisia, Strychnos,*

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[1] The species in question are: *Geniostoma angustifolium*, Bout., *G. petiolosum*, Moore et F. v. Müll.; *Labordia fagraeoidea*, Gaud., *L. glabra*, Hillebr., *L. hirtella*, Mann, *L. lophocarpa*, Hillebr., *L. membranacea*, Mann, *L. tinifolia*, Gray, *L. triflora*, Hillebr.; *Bonyunia superba*, R. Schomb.; *Antonia ovata*, Pohl; *Norrisia malaccensis*, Gardn., *N. major*, Solered.; *Strychnos pseudoquina*, St. Hil.; *Couthovia densiflora*, K. Schum.; *Fagraea auriculata*, Jack, *F. Berteriana*,

Couthovia, *Fagraea*, *Anthocleista*, *Peltanthera*, and *Nuxia*. The number of layers of hypoderm varies in the individual cases; sometimes the development of hypoderm is restricted to the upper side of the leaf, but it may be found on both sides, as for instance in most species of *Labordia* or in *Bonyunia*. There is no type of **stoma** common to the whole Order. The stomata of *Gelsemium* and *Strychnos* belong to the Rubiaceous type; those of *Gelsemium* are accompanied on either side by a single cell, those of all species of *Strychnos* by one or more cells, placed parallel to the pore. In the majority of the remaining genera the stomata are surrounded by three subsidiary cells, although more or less important deviations from this type sometimes occur in the same superficial section; in the rest of the Order, ordinary epidermal cells surround the stomata in varied numbers and without special arrangement. The stomata, as a rule, occur only on the lower side of the leaf; in the centric leaves of *Gomphostigma scoparioides* they occupy both surfaces. The approximately parallel arrangement of the stomata with regard to the median vein in *Polypremum procumbens*, L. is probably connected with the acicular shape of the leaf. The smaller **veins** are always embedded; vertically transcurrent veins have not been observed in any member of the Order. As a rule the vascular system of the veins is not accompanied by any sclerenchyma or only by a small amount; it is only in the species of *Strychnos* that a stronger development of this tissue is sometimes found in the form of a ring of sclerenchyma. Not uncommonly the bicollateral nature of the vascular bundles in the Loganioideae can be recognized in the larger veins of the leaf, as for instance in the species of *Strychnos*; but in some of these species the upper (internal) soft bast alone is developed (e.g. in *S. Castelnaei*, Wedd. or *S. acuta*, Prog.), while the lower (external) bast is entirely or almost entirely abortive. In the latter case the transverse sections of the veins have a curious appearance, their vascular system appearing inversely orientated as regards the position of the xylem and phloem. The following special features in the leaf-structure may also be mentioned: the frequent presence of fatty bodies in the assimilatory tissue, the occurrence of structures resembling cork-warts on the lower surface of the leaf in *Anthocleista nobilis*, Don., *A. inermis*, Engl., and *Fagraea Wallichiana*, Benth., and of branched sclerenchymatous cells in the tissue of the thick and fleshy leaves in species of the genera *Anthocleista*, *Fagraea*, and *Potalia*. The elements just referred to, especially those situated in the spongy tissue, belong to the category of internal hairs, since they are not in intimate connexion with the neighbouring cells on all sides, but have their arms projecting freely into the intercellular spaces of the mesophyll. Branched sclerenchymatous cells of this type are also met with in the axis of the three genera named above, occurring in the pith and primary cortex. They were found in the ground-tissue of the axis in all investigated species of these three genera; in the leaf-tissue they are absent only in *Fagraea Berteriana*, A. Gray. In this connexion it may be mentioned that more or less distinctly branched stone-cells have also been observed in the mesophyll of some species of *Strychnos* (*S. axillaris*, Colebr., *S. Benthami*, Clarke, *S. Melinoniana*, Baill., *S. pubescens*, Clarke).

In the following remarks the **hairy covering** will be described separately for the Loganioideae and the Buddleioideae. Amongst the Loganioideae simple unicellular or uniseriate hairs are found in numerous genera. It is impossible to enter into details as to their structure, which shows various types and sometimes, e.g. in *Strychnos*, has specific value. The stellate hairs of the species of

A. Gray, *F. elliptica*, Roxb., *F. fragrans*, Roxb., *F. Khasiana*, Benth., *F. lanceolata*, Bl., *F. morindaefolia*, Bl., *F. obovata*, Wall., *F. racemosa*, Jack; *Anthocleista inermis*, Engl., *A. nobilis*, Don; *Peltanthera floribunda*, Benth.; *Nuxia capitata*, Bak., *N. congesta*, R. Br., *N. coriacea*, Solered., *N. emarginata*, Sond., *N. floribunda*, Benth., *N. verticillata*, Lam.

›*igelia*, belonging to the section Tomentosae, constitute a special form of ichome; they are composed of unicellular hairs, united in tufted form and inrted upon a short, conical, multicellular pedestal. Glandular hairs are wanting ı the surface of the leaf and branch, but glandular shaggy hairs have been ›served on the leaf-base in *Strychnos* and *Fagraea*. In *Strychnos nux vomica*, L., . *lucida*, R. Br., *S. cinnamomifolia*, Thw. and others, they cover the hollows hich are found at the base of the petiole enclosing the axillary buds, and form n additional protection to the latter. The ellipsoidal head of these hairs onsists of a multiseriate central group of cells enclosing solitary crystals, ontinuous below with the short stalk and surrounded by a one-layered heath of secretory palisade-cells. A similar structure is shown by the glandular haggy hairs of *Fagraea auriculata*, Jack, which, according to Burck, serve to ıttract ants for the protection of the flowers, but here the cells of the central group are in part sclerosed, and filled with small acicular crystals, while the ›alisade-like sheathing cells form several layers and commonly contain small :lustered crystals.

In the Buddleioideae ordinary unicellular or uniseriate trichomes are not found, while glandular hairs, with flattened heads, and exclusively divided by vertical walls, are of general distribution in this tribe. The heads of these hairs consist of four or more cells (or exceptionally of a smaller number) in *Polypremum*, *Peltanthera*, and *Nuxia*, but in the remaining genera of the Buddleioideae they are two-celled. *Polypremum* has small glandular hairs, which are deeply depressed in the tissue of the leaf, and have a four-celled head. *Nuxia coriacea*, Solered. is the only species of its genus which has for the most part glandular hairs with four-celled heads, accompanied by less numerous hairs with two- or three-celled heads; other species of *Nuxia* have glandular hairs with a peltate head of more numerous cells side by side with the four-celled form, and again in other species of *Nuxia* and in the genus *Peltanthera* the former type only is present. The stalk of the glandular hairs is unicellular in the three genera referred to above, and in *Nuxia* and *Peltanthera* it is often distinguished by strong thickening of the cell-walls. In the remaining Buddleioideae (Fig. 124, *A*) the head of the glandular hairs either has an elliptical outline, in which case the division-wall between the two cells forming the head may coincide either with the greater or lesser axis of the ellipse, or it has a quadrangular outline, the four corners then being drawn out like laciniae. In addition to a stalk-cell, which has rather thick and often yellow walls, the epidermal cell from which the hair arises sometimes takes part in the formation of the stalk, inasmuch as it is raised above the level of the neighbouring cells. From the glandular hairs with a quadrangular outline, and corners drawn out as laciniae, we naturally pass on to the characteristic clothing hairs, occurring in nearly all Buddleioideae (exceptions: *Polypremum*, *Nuxia*, *Peltanthera*), and firstly the stellate hairs[1]. These **stellate hairs** consist of the ray-portion and of an almost spherical yellow-coloured stalk-cell, seated upon an epidermal cell, which is sometimes raised like a pedestal, and thus forms part of the stalk. The ray-portion is composed of two (mostly two-rayed) cells, expanded in one plane, and each with a lower tubular part which contributes to the formation of the stalk (Fig. 124, *B–C*). In certain species of *Buddleia* and *Chilianthus* (e.g. *B. salviaefolia*, Lam., Fig. 124, *D*, and *C. lobulatus*, Benth.) the stellate hairs are replaced by candelabra-hairs. These trichomes show the following characters: each tier is constructed like the ray-portion of a stellate hair—but with the difference that the two cells form

[1] The connexion between the glandular and clothing hairs is also particularly clearly demonstrated by intermediate forms, which sometimes occur on the outer side of the corolla of *Nicodemia rufescens*, Solered., and are composed of half a stellate hair and half a glandular hair.

a kind of stalk above as well as below; the cells composing the successive tiers are placed at right angles to one another, and the tiers are united by almost spherical cells with yellow walls. It may be added that the stellate hairs may either have thick walls and narrow lumina, as in *Chilianthus dysophyllus*, Benth., *Buddleia americana*, L., *Adenoplea sinuata*, Radlk., and *Nicodemia diversifolia*, Ten., or wide lumina and relatively thin walls, as in *Adenoplusia axillaris*, Radlk., and that the cells of the ray-portion may sometimes (e. g. in *Buddleia americana*) show more than two rays. If one imagines the surface which bears the rays in these many-rayed stellate hairs to be increased, small scales (Fig. 124, *E*) would result, such as have been observed in

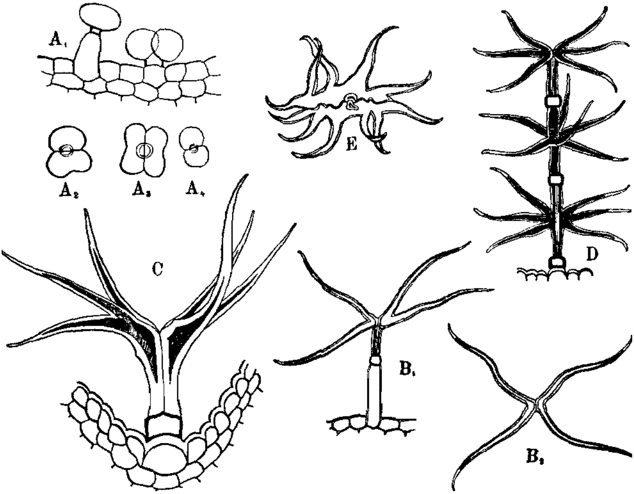

FIG. 124. Hairy covering of the Buddleioideae: A_1–A_4, Glandular hairs of *Buddleia americana*, L.: A_1, in transverse section, A_2–A_4, in surface-view; B_1–B_2, four-armed stellate hair of the same species, B_1, seen from the side, B_2, in surface-view; C, six-rayed stellate hair of the same species. D, Candelabra-hair of *Buddleia salviaefolia*, Lam. E, Peltate hair of *Gomphostigma scoparioides*, Turcz.—Original.

Gomphostigma scoparioides, Turcz. and *G. incanum*, Oliv., *Chilianthus arboreus*, Benth. and within the genus *Buddleia* ('*B. lanceolata*, Benth., J. D. Smith, n. 2148, Guatemala'). The division-line between the two cells of the scale has an undulated course in *Gomphostigma*, elsewhere it is straight. Lastly, we may mention the peculiar branched hairs of *Nuxia emarginata*, Sond.; they have a kind of sympodial structure, inasmuch as the basal part of each hair-cell belongs to the main axis of the trichome, whilst the apical portion forms a lateral branch.

Oxalate of lime is excreted in various forms, as has been explained above. Clustered crystals are common, and may be accompanied by solitary crystals or

some other form of oxalate of lime in the same species. Special mention may be made of the large clustered crystals occurring in correspondingly large cells of the mesophyll (species of *Strychnos*, *Usteria guineensis*, Willd.), and the clustered crystals in the veins of the leaf of *Strychnos Martii*, Prog. and *S. parvifolia*, A.DC., which cause the 'nervuli scabro-punctulati' of systematists and afford a ready means of distinction between the species named and other very similar species (*S. brasiliensis*, Mart. and *S. breviflora*, A. DC.). Except in *Strychnos*, the ordinary large solitary crystals are in fact rare (species of *Mostuea*, *Gardneria*) in this Order, and a true sheathing of the veins with solitary crystals is found in *Strychnos* only. Smaller (sometimes minute) and variously shaped solitary crystals are commoner (species of *Geniostoma*, *Labordia*, *Polypremum*, *Adenoplusia*); small acicular crystals are still more frequently met with (species of *Logania*, *Spigelia*, *Fagraea*, *Potalia*, *Anthocleista*, *Peltanthera*, *Nuxia*, *Gomphostigma*, *Chilianthus*, *Buddleia*). Typical crystal-sand is characteristic of the genus *Couthovia*, where it is found in the axis and leaf. The occurrence of small crystalline granules, which are met with in the same cell as an ordinary solitary crystal (for example, in many species of *Strychnos*) must not be confused with this. Styloids have been observed in the bast and primary cortex of *Usteria* (side by side with clustered crystals in the axis and leaf) and in the interxylary phloem of *Bonyunia* (side by side with clustered crystals in the pith). Finally, styloid-like crystals, viz. twin crystals, combined in the shape of a V, but at a more obtuse angle, are characteristic of a group of very closely related species of *Strychnos* (*S. brasiliensis*, Mart., *S. breviflora*, A. DC., *S. Grayi*, Griseb., *S. macroacanthos*, Prog., *S. micrantha*, Spruce, *S. nigricans*, Prog., *S. Poeppigii*, Prog., *S. subpenninervis*, Solered., Martius, Obs. n. 3061 in Herb. Monac.) and can be recognized even with a lens as transparent dots.

3. Structure of the Axis. It may again be specially pointed out that all the genera of the Loganioideae have bicollateral vascular bundles, while all the Buddleioideae have simple collateral bundles. The **intraxylary soft bast** is variously differentiated in the individual species of the Loganioideae. It either forms a ring completely surrounding the pith, or isolated bundles of soft bast are situated opposite all or some of the vascular bundles of the branch. In very many cases the intraxylary phloem undergoes secondary growth by means of a cambium.

Regarding the structure of the **pith** it may be mentioned that the cells of this tissue are in many cases unlignified, but that in certain species of *Strychnos* groups of stone-cells occur, while in certain species of *Gardneria*, *Couthovia*, *Spigelia*, and *Usteria*, there are elongated, sclerenchymatous parenchyma-cells, and in the species of *Fagraea*, *Potalia*, and *Anthocleista* branched sclerenchymatous cells.

The structure of the **wood** may be described as follows. The vessels, as might be expected, vary greatly in their diameter, which is very small in a large number of cases. The perforations of the vessels are exclusively of the simple type in almost all the genera. Species of *Geniostoma*, *Labordia*, and *Mitreola*, alone form exceptions; in these plants scalariform perforations with few bars or malformed scalariform perforations also occur, but in subordinate numbers. Spiral thickening of the vessel-wall has been observed in *Logania floribunda*, R. Br., *L. angustifolia*, Sieb., *L. linifolia*, Schlecht., *Chilianthus arboreus*, Benth., *Buddleia macrostachya*, Benth., *Gomphostigma scoparioides*, Turcz., *Nuxia floribunda*, Benth., and *Nicodemia diversifolia*, Ten. The vessel-walls, where they are in contact with parenchyma, have ordinary bordered pitting; in the genera *Fagraea*, *Gomphostigma* and *Buddleia*, we find bordered pits accompanied by others transitional to simple pits. The wood-parenchyma is, as a rule, only developed to a small extent. A more abundant development of this tissue occurs only in certain species of

Strychnos and *Fagraea*. The medullary rays of the wood are invariably narrow, attaining at the utmost a breadth of four cells (*Anthocleista inermis*, Engl.). The wood-prosenchyma has either thick walls and narrow lumina, or thinner walls and correspondingly wider lumina, and bears either bordered or simple pits. The nature of the pitting of the wood-prosenchyma is not always easy to determine. According to my investigations, the prosenchyma has bordered pits in *Gelsemium*, *Mostuea*, *Usteria* (typical ?), *Bonyunia* (typical ?), *Antonia* (typical ?), *Norrisia* (typical ?), *Strychnos*, *Couthovia* and *Polypremum*; on the other hand, it has simple pits in *Coinochlamys*, *Logania* (here the same applies to numerous tracheids as well), *Geniostoma*, *Labordia*, *Spigelia*, *Mitreola*, *Mitrasacme*, *Gardneria*, *Fagraea*, *Potalia*, *Anthocleista*, *Peltanthera*, *Nuxia*, *Gomphostigma*, *Chilianthus*, *Buddleia*, *Adenoplusia* and *Nicodemia*. Septation of the simple-pitted wood-prosenchyma has been observed in species of *Coinochlamys*, *Geniostoma*, *Labordia*, *Fagraea*, *Peltanthera* and *Nicodemia*.

The structure of the **cortex** also affords valuable characters for special diagnosis. In the Loganioideae the origin of the cork is superficial in all investigated cases [1]. Of the Buddleioideae only the two genera *Polypremum* and *Peltanthera*, which are somewhat anomalous in other respects also, agree with the Loganioideae in this feature. The remaining genera [2] of the Buddleioideae exhibit pericyclic development of cork. In the superficial origin of the cork it is usually the outermost cell-layer of the primary cortex which becomes the phellogen, more rarely the epidermis itself (*Spigelia glabrata*, Mart. and certain species of *Strychnos*) or a somewhat deeper layer of the primary cortical parenchyma (certain species of *Strychnos* and *Logania*). In the case of pericyclic origin of the cork, the phellogen appears internally to a concentric zone, defined by groups of sclerenchyma, at the outermost margin of the soft bast. In all cases the cork-cells usually have wide lumina, the walls being either thin or thick; cells, sclerosed on one side only, are met with in the cork of species of *Strychnos* and *Geniostoma*, as well as in *Bonyunia superba*, R. Schomb.; stone-cells are found in the cork in species of *Fagraea*. A distinctly peculiar kind of cork, which I call lamellated cork (Fig. 125), is characteristic of the genera *Geniostoma*, *Labordia*, and *Couthovia*. In the formation of this tissue the successive cell-layers of the primary cortex, commencing with the outermost layer, develop in turn into cork-cambium; each phellogen only produces a few (1 or 2) layers of cork-cells, and then becoming extinct, is itself transformed into cork-cells. The individual lamellae of the lamellated cork thus correspond to the 2–3 layers of cork-cells, formed by the activity of each phellogen; in the individual lamellae the cork-cells of the outermost layer have the widest lumina; the remainder are compressed in a radial direction. In a certain number of the species of the genus *Geniostoma* (*G. angustifolium*, Bout., *G. parviflorum*, Boj., *G. pedunculatum*, Boj.), in which each lamella of the cork consists of only two layers of cells, the inner of these two layers consists of cells sclerosed and pitted on the inner tangential and the radial walls.

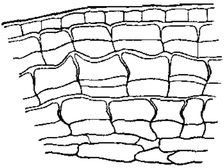
FIG. 125. Lamellated cork of *Geniostoma rupestre*, Forst.—Original.

As regards the remaining features in the structure of the cortex, the most important fact is, that a composite, continuous, sclerenchymatous ring does not

[1] These are: *Logania*, *Geniostoma*, *Labordia*, *Spigelia*, *Antonia*, *Norrisia*, *Strychnos*, *Couthovia*, *Fagraea*, *Anthocleista*.

[2] The following genera have been investigated with regard to this particular: *Nuxia*, *Gomphostigma*, *Chilianthus*, *Emorya*, *Buddleia*, *Adenoplusia* and *Nicodemia*.

ur at the outer limit of the bast in any member of the Order. In place of this, re are either groups of sclerenchymatous rod-cells (species of *Labordia*, *Fagraea*, *ltanthera* and *Nicodemia*), or sclerenchymatous fibres, which may occur in all numbers or in the form of isolated bundles, or lastly, may constitute a se ring, and are sometimes associated with sclerenchyma of the rod-cell pe (species of *Gelsemium*, *Logania*, *Geniostoma*, *Labordia*, *Spigelia*, *Mitreola*, *teria*, *Gardneria*, *Strychnos*, *Couthovia*, *Fagraea*, *Potalia*, *Polypremum*, *Nuxia*, *mphostigma*, *Chilianthus*, *Buddleia* and *Adenoplusia*); in a third series of ses no sclerenchyma is present at the outer limit of the bast (species of *Coino-lamys*, *Mostuea*, *Logania*, *Geniostoma*, *Mitreola*, *Mitrasacme*, *Bonyunia*, *Antonia*, *orrisia*, *Strychnos*, *Couthovia*, *Fagraea* and *Anthocleista*). The occurrence of anched sclerenchymatous cells in the primary cortical parenchyma is charac-ristic of the genera *Fagraea*, *Potalia* and *Anthocleista*. Ordinary stone-cells e not uncommonly present in the primary cortex (e. g. in *Geniostoma parvi-rum*, Boj., *Labordia fagraeoidea*, Gaud., &c.); in *Logania serpyllifolia*, R. Br. r., *Geniostoma ovatum*, Boj., *Spigelia Olfersiana*, Ch. et Schl., and other species ey are elongated in the vertical direction after the manner of rod-cells. True ratification of the bast by means of bast-fibres has not been observed in any ember of the Order. On the other hand, sclerenchymatous cells, resembling d-cells, occur in the bast in many cases, e. g. *Geniostoma ovatum*, Boj. and . *Cumingianum*, Benth., *Labordia fagraeoidea*, Gaud. and *L. lophocarpa*, lillebr., &c. It may be added that the majority of the species of *Strychnos* ossess a ring of stone-cells in the cortex; this ring is situated in the middle of ne primary cortex in a certain number of the species, whilst in some others it es in the outermost portion of the bast. In the latter case the ring of stone-ells is usually only separated from the primary bast-fibres, marking the uter limit of the phloem, by small groups of soft bast, in which it has been hown that sieve-tubes occur. The absence of a ring of stone-cells is charac-eristic of certain species of *Strychnos*, while others are distinguished by the resence of this tissue, either in the bast or in the primary cortex.

I. The ring of stone-cells is wanting in the cortex of: *Strychnos aculeata*, Solered., *S. breviflora*, A. DC., *S. Grayi*, Griseb., *S. micrantha*, Spruce, *S. nigricans*, Poepp., *S. Poeppigii*, Prog. (here there are only isolated groups of stone-cells internal to the primary hard bast), *S. subpenninervis*, Solered. II. The ring of stone-cells is found in the outermost portion of the bast in *S. angustiflora*, Benth., *S. Barteri*, Solered., *S. brasiliensis*, Mart., *S. cinnamomifolia*, Thw., *S. Gaultheriana*, Pierre, *S. lucida*, R. Br., *S. Maingayi*, Clarke var. *fructuosa*, Clarke, *S. nux vomica*, L., *S. ovalifolia*, Wall., *S. potatorum*, L. fil., and *S. Tieute*, Lesch. III. The ring of stone-cells is found in the middle of the primary cortex in: *S. acuminata*, Wall. emend. Clarke, *S. acuta*, Prog., *S. albiflora*, Prog., *S. Atherstonei*, Harv., *S. axillaris*, Colebr., *S. Beddomei*, Clarke, *S. Benthami*, Clarke, *S. bracteata*, Ruiz et Pav., *S. brevifolia*, Spruce, *S. Castelnaei*, Wedd., *S. chlorantha*, Prog., *S. Dalzellii*, Clarke, *S. Erichsonii*, R. Schomb., *S. Gardneri*, A. DC., *S. glabra*, Prog., *S. hachensis*, Karst., *S. hirsuta*, Spruce, *S. Horsfieldiana*, Miq., *S. innocua*, Del., *S. lanceolaris*, Miq., *S. lanceolata*, Spruce, *S. laurina*, Wall., *S. laxa*, Solered. (here in addition there is a phellodermal ring of stone-cells), *S. Maingayi*, Clarke, *S. malaccensis*, Benth., *S. Martii*, Prog., *S. Mediola*, Sagot, *S. Melinoniana*, Baill., *S. monosperma*, Miq., *S. multiflora*, Benth., *S. palembanica*, Miq., *S. paniculata*, Champ., *S. parvifolia*, A. DC., *S. pedunculata*, Benth., *S. pseudoquina*, St. Hil., *S. psilosperma*, F. v. Müll., *S. pubescens*, Clarke, *S. rondeletioides*, Spruce, *S. Rouhamon*, Benth., *S. rubiginosa*, A. DC., *S. rufa*, Clarke, *S. rufescens*, Solered. (Kappler n. 2148, Surinam), *S. septemnervis*, Clarke, *S. smilacina*, Benth., *S. spinosa*, Lam. (here in addition there is a phellodermal ring of stone-cells), *S. subcordata*, Spr., *S. Thwaitesii*, Solered., *S. tomentosa*, Benth., *S. toxifera*, Schomb., *S. trinitensis*, Griseb., *S. triplinervia*, Mart., *S. Wallichiana*, Benth.

To conclude the description of the axis we have still to deal with such **structural anomalies** as occur in the Order, excepting the bicollateral nature of

the vascular bundles, which has already been discussed in detail; these anomalies are as follows: medullary groups of soft bast or medullary vascular bundles, cortical bundles and interxylary phloem. Medullary groups of soft bast are found in the two very closely related genera *Antonia* and *Norrisia*, medullary and cortical vascular bundles in *Anthocleista* (*A. inermis*, Engl.). The cortical bundles of *Anthocleista* have concentric structure with central xylem. Interxylary soft bast has been shown to occur in the monotypic genus *Antonia*, in both species of *Norrisia*, in the monotypic genus *Bonyunia*, in very many species of *Strychnos*, and finally in *Logania serpyllifolia*, R. Br. var. *angustifolia*, Benth. (Preiss n. 1242, Nov. Holl.). It is still an open question whether the islands of soft bast in the wood are characteristic of the entire genus *Strychnos*, but it is not impossible that this may be the case, according to my own investigations. As will be stated more fully elsewhere, I have only been able to prove the occurrence of islands of soft bast in herbarium-material, in a certain number of the species and not in the remainder. Even the investigation of herbarium-material has however shown that in certain species (such as *S. rondeletioides*, Spruce, *S. pseudoquina*, St. Hil., *S. Gardneri*, A. DC., *S. Rouhamon*, Benth., or *S. glabra*, Prog.) the soft bast only appears in the later growth of the wood, while suitable material of the stem and branch of *S. monosperma*, Miq., which I obtained through Treub from the Buitenzorg garden, showed that the interxylary phloem may sometimes make its appearance even at a very late stage; and this was confirmed by studying the structure of a thick axis of *S. Castelnaei*, Wedd. (in the wood-collection of the Museum at Munich). But it was possible to draw a further conclusion, though with a certain amount of reserve, from the abundant material I had for investigation, namely that the early or late appearance (or possibly the absence) of the islands of soft bast is of value for specific diagnosis. In this respect the following statements possess more than a merely statistical value.

Islands of soft bast have been observed in the wood in herbarium-material of: *Strychnos acuminata*, Wall. emend. Clarke, *S. angustiflora*, Benth., *S. Atherstonei*, Harv., *S. Beddomei*, Clarke, *S. cinnamomifolia*, Thw., *S. Erichsonii*, R. Schomb., *S. Gardneri*, A. DC., *S. Gaultheriana*, Pierre, *S. glabra*, Prog., *S. Horsfieldiana*, Clarke, *S. hypogyna*, Clarke, *S. innocua*, Del., *S. lanceolaris*, Miq., *S. laurina*, Wall., *S. lucida*, R. Br., *S. Maingayi*, Clarke (incl. var. *fructuosa*, Clarke), *S. multiflora*, Benth., *S. nux vomica*, L., *S. ovalifolia*, Wall., *S. paniculata*, Champ., *S. Poeppigii*, Prog., *S. potatorum*, L. fil., *S. pseudoquina*, St. Hil., *S. rondeletioides*, Spruce, *S. Rouhamon*, Benth., *S. rufa*, Clarke, *S. septemnervis*, Clarke, *S. smilacina*, Benth., *S. subcordata*, Spruce, *S. Thwaitesii*, Solered., *S. Tieute*, Lesch. and *S. Wallichiana*, Benth.

Islands of soft bast could not be demonstrated in herbarium-material of: *S. aculeata*, Solered., *S. acuta*, Prog., *S. albiflora*, Prog., *S. axillaris*, Colebr., *S. Barteri*, Solered., *S. Benthami*, Clarke, *S. brachiata*, Ruiz et Pav., *S. brasiliensis*, Mart., *S. breviflora*, A. DC., *S. brevifolia*, Spr., *S. Castelnaei*, Wedd., *S. chlorantha*, Prog., *S. Dalzellii*, Clarke, *S. Grayi*, Griseb., *S. hachensis*, Karst., *S. hirsuta*, Spruce, *S. lanceolata*, Spruce, *S. laxa*, Solered., *S. malaccensis*, Benth., *S. Martii*, Prog., *S. Medeola*, Sagot, *S. Melinoniana*, Baill., *S. micrantha*, Spruce, *S. monosperma*, Miq., *S. nigricans*, Poepp., *S. palembanica*, Miq., *S. parvifolia*, A. DC., *S. pedunculata*, Benth., *S. psilosperma*, F. v. Müll., *S. pubescens*, Clarke, *S. rubiginosa*, A. DC., *S. rufescens*, Solered., *S. spinosa*, Lam., *S. subpenninervis*, Solered., *S. tomentosa*, Benth., *S. toxifera*, Schomb., *S. trinitensis*, Griseb., and *S. triplinervia*, Mart.

As to the occurrence of the interxylary phloem in *Logania serpyllifolia* var., I only found a single lamella of soft bast (with sieve tubes) in the wood of the piece of branch examined. The development of the interxylary phloem has only been followed in detail in the genus *Strychnos*. Contrary to the statements of the earlier observers (De Bary, Van Tieghem) it has been shown by Herail, Scott and Brebner, Chodat, H. Schenck and Sauvan that the islands of soft bast in the wood are formed by the cambium on its outer side, and that after the formation of these islands the strips of cambium opposite them cease to be

active; the cambial ring, which thus becomes interrupted, is ultimately repaired by the production of complementary strips of cambium on the outer side of the islands of soft bast.

NOTE.—As regards the structure of the **root**, it is a noteworthy fact that in the genus *Strychnos*, in *S. spinosa*, according to Scott and Brebner, and in *S. nux vomica*, according to Van Tieghem, medullary bundles of phloem subsequently arise internally to the primary xylem-groups. The interxylary phloem-strands also appear to be present in the wood of the root.

APPENDIX.

The anatomy of the **two anomalous genera** *Desfontainea* and *Plocosperma* will be shortly described here.

The genus *Desfontainea* (*D. spinosa*, Ruiz et Pav.) is specially characterized by the simple collateral structure of the vascular bundles and by the scalariform perforations with numerous bars in the vessels, this being the only type of perforation present. The wood shows: narrow medullary rays; vessels with small lumina and with their walls provided with bordered pits, even where they are in contact with parenchyma; and wood-prosenchyma with rather distinct bordered pits. The cork, which arises at some depth below the epidermis, near the internal margin of the bast, contains stone-cells in some cases. The leaf-structure of *Desfontainea* presents no special features; it is bifacial. The stomata do not possess any special subsidiary cells. Crystalline elements, trichomes, as well as internal glands, are wanting throughout the plant.

The second anomalous genus *Plocosperma*, with its two species *P. buxifolium*, Benth. and *P. microphyllum*, Baill. MS., is distinguished by the absence of bicollateral vascular bundles and by the possession of trichomes of a special type. Firstly, there are small club-shaped, glandular hairs, projecting above the epidermis as a bicellular structure, in which one cell may be considered to be the stalk, and the other the glandular head; secondly, simple, unicellular hairs occur, which are filled with carbonate of lime, while the cells adjoining them exhibit cystolith-like bodies, encrusted with lime, as in many Boragineae and Hydrophyllaceae. The leaf-structure is bifacial. The stomata have no special subsidiary cells. The vascular bundles of the veins are provided with a strong sclerenchymatous sheath. Finally, small clustered crystals are found accompanying the sclerenchyma of the veins, and styloids occur in the bast of the axis.

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[1] The wood, there described as *Strychnos colubrina*, can scarcely belong to a species of *Strychnos*.

GENTIANEAE.

This Order may be divided into two groups, according to the anatomical features of the axis; the first of these groups includes the tribes Exaceae, Chironieae and Swertieae, while the second consists of the Menyantheae. Bicollateral vascular bundles are on the whole[1] characteristic of the first three tribes, whilst simple collateral bundles are distinctive of the Menyantheae. Regarding the structure of the wood, it may be noted that the medullary rays are narrow, or may be absent, that the vessels generally have simple perforations only, and that the wood-prosenchyma is provided with more or less typically differentiated bordered pits. A special type of stoma does not occur. Oxalate of lime and internal secretory elements are wanting. On the other hand, the Gentianeae are distinguished as regards their chemical constituents by the invariable presence of bitter substances in all parts of the plant. A hairy covering is rarely present, and consists solely of simple hairs. Special features observed in this Order are the characteristic intercellular hairs of many Menyantheae and the islands of soft bast in the wood of the axis in *Chironia, Orphium, Erythraea, Ixanthus* and *Gentiana*.

The structure of the **leaf** has been examined by Bötticher in the more widely distributed genera[2], and in greater detail in the case of the Menyantheae by Perrot. The leaf-structure is very uniform, and is bifacial or centric. The stomata are usually present on both sides of the leaf, and may either be isolated or very numerous on the upper side; in the floating leaves of *Limnanthemum* they are found on the upper side only. Their neighbouring cells are commonly differentiated from the other epidermal cells. In the Menyantheae the mother-cell of the guard-cells is cut off by the first division-wall.

Crystals of **oxalate of lime** have not been observed by any author either in the axis or leaf; but crystalloids have been found in the nuclei in the leaf-tissue of *Limnanthemum nymphaeoides* and *Menyanthes trifoliata* (Zimmermann). An excretion of wax occurs on the surface of leaf and stem in *Chlora perfoliata* (Bötticher), and a deposition of mucilage takes place in the intercellular spaces in the cushion-like swellings of the leaf-base in *Gentiana acaulis* and *G. imbricata* (Lazniewski). The **internal hairs** mentioned above are branched, thick-walled cells, which have pointed arms projecting into the intercellular spaces; they occur in the parenchyma of the leaf, stem and root. Perrot met with them in *Limnanthemum, Liparophyllum* and species of *Villarsia*, whereas they are wanting in *Menyanthes, Nephrophyllidium* and some species of *Villarsia*, according to the same author. A well-developed **hairy covering** only occurs in *Orphium*. The trichomes of *Orphium frutescens*, E. Mey. are simple uniseriate hairs composed of a few cells and with a blunt terminal cell. Uniseriate hairs secreting mucilage have been observed by Schilling on the buds in species of *Menyanthes* and *Limnanthemum*. Finally the hydathodes on the margin of the leaf in the Menyantheae and the peculiar cell-groups found in the lower epidermis of the species of *Limnanthemum* and of some species of *Villarsia* also deserve mention. The former consist of the termination of a vascular bundle provided with epithema and contain stomata in the overlying epidermis. The latter occur on a raised portion of the leaf-surface of varying size, and their function is unknown.

The structure of the **petiole** has only been investigated in *Menyanthes trifoliata* and *Limnanthemum nymphaeoides*. The characteristic region in both

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[1] The only exceptions are species of the saprophytic genera *Voyria* and *Leiphaimos*.

[2] These are: *Exacum, Sebaea; Chironia, Enicostema, Curtia, Chlora, Erythraea, Sabbatia, Ixanthus, Dejanira, Cicendia, Canscora, Schultesia, Coutoubea, Lisianthus; Gentiana, Pleurogyne, Swertia, Halenia, Bartonia; Menyanthes, Villarsia, Limnanthemum.*

cases contains isolated vascular bundles, the number of these being ten and five respectively.

The bicollateral nature of the **vascular bundles** has been re-examined by Gilg (in relation to the statements of Vesque, Solereder and Bötticher) in representatives of all the genera with the exception of *Cotylanthera, Voyriella* and *Lagenanthus*, and was demonstrated by him in every case apart from those previously mentioned as exceptions. According to Gilg, the intraxylary phloem in most cases forms a narrow, continuous belt; in other cases there are small groups situated at the margin of the pith, and sometimes easily overlooked. According to Scott and Brebner, medullary phloem-groups sometimes (*Gentiana acaulis*) arise as branches of the intraxylary phloem. Sclerenchyma rarely accompanies the internal soft bast.

In the following statements on the structure of the **wood**, the woody species of *Tachiadenus, Chironia, Orphium, Coutoubea, Prepusa* and *Lisianthus*, investigated by me, are taken into special consideration. A transverse section of the wood shows vessels with rather small lumina (maximum diameter=·04 mm.), and medullary rays, which are usually narrow (1–2 cells in breadth), the cells being elongated in the vertical direction. Bötticher mentions the absence of medullary rays in species of *Cicendia, Schultesia*, and *Ophelia*. The perforations of the vessels are usually simple; but accompanying this type scalariform perforations with 1 or 2 bars frequently occur, or malformed perforations, in which the division-wall is perforated in an irregular manner, e. g. in *Chironia baccifera*, L., *Orphium frutescens*, E. Mey. and *Coutoubea ramosa*, Aubl. The walls of the vessels in the species investigated by me bear bordered pits, where they are in contact with parenchyma of the medullary rays. The wood-parenchyma is invariably developed in small quantity. In my 'Holzstruktur' the wood-prosenchyma is stated to bear bordered pits in which the border is frequently smaller than the opening, or the bordered pits are indistinct owing to the thick walls and narrow lumina of the elements (*Prepusa montana*, Mart.). Though Gilg confirms these observations, Bötticher states that in all species investigated by him and belonging to the first three tribes, he met with prosenchyma bearing bordered pits accompanied by prosenchyma with simple pits, the latter being present in varied abundance and often forming the groundwork of the wood.

The **primary cortex** contains collenchymatous tissue in many cases. In the pericycle a ring of mechanical tissue may or may not be present. The cork in the few cases investigated develops 'beneath the cortical parenchyma,' according to Bötticher.

Interxylary phloem was first demonstrated in the axis by Vesque in *Chironia* and by me in *Orphium frutescens*, E. Mey. In the genus *Chironia* it seems to be of quite general occurrence, according to recent investigations (Gilg, Scott and Brebner, Bötticher). In both genera the interxylary groups of soft bast are produced on the inner side by the cambium, and the mode of origin is the same in the interxylary phloem-islands, described in the root of *Gentiana lutea* almost simultaneously by Arthur Meyer and J. E. Weiss, in the root of *G. pannonica, G. punctata* and *G. purpurea*, by Arthur Meyer, in that of *G. cruciata* by Jost, in that of species of *Erythraea* by Chodat and Bötticher, and in that of *Ixanthus viscosus* by Bötticher. The root of *Chironia peduncularis*, Lindl.[1] has

[1] According to Scott and Brebner the root-structure of *Chironia peduncularis* shows the further peculiarity that the cambium of the root is first developed on the inner side of the primary vessels (protoxylem). Subsequently the protoxylem becomes embedded in the secondary xylem produced by the activity of the cambium, since the corresponding strip of cambium ceases its activity, and the cambial ring which is thus interrupted is supplemented by a meristematic arc, originating externally to the protoxylem.

interxylary and intraxylary phloem, both of these being in connexion with the interxylary phloem of the stem (Scott and Brebner).

The structure of the axis of the inflorescence in the species of *Limnanthemum*, belonging to the section *Nymphaeanthe*, is also anomalous according to Goebel, Gilg and Perrot. Whereas the only species of the section *Waldschmidtia*, viz. *L. nymphaeoides*, exhibits normal dicotyledonous structure, the manner of distribution of the vascular bundles in *L. cristatum*, *L. Humboldtianum*, *L. indicum* and others calls to mind a monocotyledonous stem, since a large vascular bundle occurs in the centre and numerous smaller bundles lie scattered at the periphery.

Bötticher states that **cortical vascular bundles** occur in the axis of *Menyanthes trifoliata*.

The structure of the stem in the two **saprophytic genera** *Voyria* and *Leiphaimos* now remains to be discussed. The entire shoot of *Voyria*, including the whole floral region, is distinguished by the complete absence of stomata (Johow). The stem shows a few (4–6) isolated vascular bundles arranged in a ring in transverse section; according to Johow these bundles have concentric structure (with central xylem) and are perhaps of the nature of steles in *V. tenella*, *V. trinitensis* and *V. uniflora*, whilst in *V. rosea* they are bicollateral according to Gilg [1]. According to Gilg an undetermined species of *Leiphaimos* has a single concentric vascular bundle, the xylem of which is slightly developed and occupies a central position.

Literature: Grisebach u. Hoffmann, Luftröhrenh. bei *Limnanthemum*, Linnaea, Bd. xii, 1838, pp. 682–5 and Taf. vii; see also Linnaea, Bd. xiii, 1839, p. 291.—Vesque, Anat. de l'écorce, Ann. sc. nat., sér. 6, t. ii, 1875, pp. 143 and 146 and pl. 10.—Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 52 and 349.—Areschoug, Bladets Anat., Minnesskrift Lund, 1878, p. 78 et seq. and Tab. ix.—J. E. Weiss, in Flora 1880, p. 89.—Petersen, in Engler, Bot. Jahrb., Bd. iii, 1882, pp. 384, 385.—A. Meyer, *Gent. lutea* etc., Arch. d. Pharm. 1883, pp. 502 and 569 et seq.—J. E. Weiss, in Bot. Centralbl. 1883, iii, p. 410.—Solereder, Holzstr., 1885, pp. 182, 183.—Johow, in Pringsheim Jahrb., Bd. xvi, 1885, p. 415 et seq. and Tab. xvi to xviii.—Petit, Pétiole, Act. Soc. Linn. de Bordeaux, t. 43, 1889, pp. 29, 30 and pl. i.—Jost, in Bot. Zeit. 1890, p. 442.—Goebel, in Ann. jard. bot. de Buitenzorg, vol. ix, 1891, pp. 120–6 and pl. xvi.—Scott and Brebner, Internal phloëm etc., Ann. of bot., vol. v, 1891, pp. 277 and 287 et seq. and pl. xviii.—Zimmermann, Pflanzenzelle, 2. Heft, 1891, p. 129.—Solereder, in Natürl. Pflanzenfam., ii. Teil, Abt. 3, 1892, p. 27.—Chodat, in Rep. of Congress, Genoa, separate copy, 1893, p. 12.—Schilling, Schleimbild., Flora 1894, pp. 313–19.—W. Boetticher, Vergl. Anat. d. G., Diss., Erlangen, 1895, 62 pp.—Gilg, in Natürl. Pflanzenfam., iv. Teil, Abt. 2, 1895, pp. 52, 53.—Lazniewski, Alpenfl., Diss., München, 1896, p. 38 et seq.; also in Flora 1896.—Perrot, Anat. des Menyanthées, Bull. Soc. bot. de France 1897, pp. 340–54 and pl. xii; see also Journ. de bot. 1897, pp. 195–7.—Warming, Halofyt Stud., K. Danske Vid. Selsk. Skr. 1897, p. 186.—[Holm, *Obolaria virginica*, L., Ann. of bot., vol. xi, 1897, pp. 369–83 and pl. xix.]

POLEMONIACEAE.

The essential anatomical features of this Order are as follows: The vascular bundles of the stem are simply collateral in structure. When secondary xylem-vessels are present they possess simple perforations. The cork when present appears in the outer layers of the cortex or at the outer limit of the phloem. Oxalate of lime appears to be absent, but well-developed, spindle-shaped and calcified cystoliths have been met with in the cortex of the root in a plant described as *Phlox carolina* (Greenish [2]). The stomata, as far as is known, are surrounded by an indefinite number of ordinary epidermal cells. The hairy covering consists of (*a*) simple, uniseriate, and (*b*) glandular hairs.

Very little is known as to the **leaf-structure**. In order to be able to say something about the stomata, I examined the leaves of *Loeselia coccinea*, Don, *Cobaea scandens*, Cav., and *Polemonium caeruleum*, L. (see above). I found no trace of oxalate of lime in these leaves.

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[1] It may be added that the root of *Voyria* has an endotrophic mycorrhiza.

[2] Greenish, *Phlox carolina*, Pharm. Journ. and Transact. 1891, pp. 839 to 840.

The **petiole** of *Cobaea scandens*, investigated by Petit[1], shows a semilunar vascular bundle in the characteristic region, and above this bundle small groups of soft bast and a smaller vascular strand are situated.

The **stem-structure** of the Polemoniaceae is more thoroughly known, owing to Schlepegrell's work[2], which deals with all the eight genera, and Peter's statements in the 'Natürliche Pflanzenfamilien[3].' The vascular bundles of the branch, as stated above, have a simple collateral structure in all cases. The wood of the two species, *Loeselia coccinea*, Don, and *Collomia stenosiphon*, Kunze, investigated by me[4], shows (*a*) vessels with lumina of moderate size (diameter reaching ·04 mm.) and a prevailing radial arrangement, and (*b*) uniseriate medullary rays. Vessels with large lumina are only present in *Cobaea scandens*. The perforations of the vessels are in general simple in the cases investigated (species of *Cobaea*, *Collomia*, *Loeselia*, and *Phlox*); in *Loeselia coccinea*, as an exceptional occurrence, I have met with scalariform perforations with one bar. The wood-prosenchyma, in the two species investigated by me, has simple pits or slit-shaped pits with indistinct and small borders; it is septate in *Loeselia coccinea*. The soft bast in general consists of small cells, and either constitutes a continuous layer in the usual way, or occurs in the form of cell-groups, enclosed like nests, owing to the cortical tissue, external to the soft bast, becoming lignified and united to the xylem-mass in places (e.g. in *Phlox paniculata*, L., *P. divaricata*, L., and *Gilia densiflora*, Benth.). Intercellular spaces, containing yellow masses of secretion, were observed by Peter in the phloem of *Cobaea scandens*, Cav., but they still require further examination. According to Peter, bast-fibres, either isolated or united into groups, sometimes occur on the outer side of the bast (e.g. in *Gilia coronopifolia*, Pers., and *Phlox aristata*, Michx.), or in their place a closed ring of bast-fibres is found (*Collomia heterophylla*, Hook., *C. grandiflora*, Dougl., *Phlox longifolia*, Nutt., *P. Douglasii*, Hook., *P. acuminata*, Pursh, and *Gilia capitata*, Dougl.); in other cases again a starch-sheath is present. In the primary cortex, as also in the pith, sclerosis of more or less numerous cells commonly takes place. Collenchyma frequently appears in the primary cortex (quite typical for example in *Phlox maculata*, L., or *Polemonium pauciflorum*, Wats.), while cells with membranes which may become much swollen appear to occur in this region in *Phlox Hoodii*, Rich., according to Peter. Peter describes the development of cork in *Phlox Stellaria*, Gray, as taking place 'in the outer layers of the cortex,' whilst Schlepegrell found it to commence at the outer limit of the phloem in other species of *Phlox* (*P. subulata*, &c.). At this point we may mention that neither Peter nor Schlepegrell records the presence of solitary or clustered crystals of oxalate of lime in the stem.

The **hairy covering** consists of simple uniseriate hairs and of glandular hairs. According to Schlepegrell, the simple hairs of *Phlox maculata* show a tendency to assume a branched form, one or other of the cells of the hair having a lateral protrusion resembling a branch. Glandular hairs are stated by Schlepegrell to occur in species of *Phlox*, *Gilia*, *Polemonium*, *Loeselia*, *Bonplandia*, and *Cantua*, but no further details are given, or at any rate the description is insufficient. I must therefore confine my remarks to the glandular hairs of *Gilia tricolor* and *Collomia linearis*, described by Martinet[5], and to those of *Loeselia coccinea*, Don, which I have examined myself. *Gilia tricolor* has glandular hairs with a long stalk, consisting of a row of cells which are shorter towards the apex and have rather thick walls. The head in these glands is ellipsoidal and becomes divided up by two, four, or eight vertical walls into a corresponding number of cells. Similar

[1] Petit, Pétiole, Mém. de la Soc. des sc. phys. et nat. de Bordeaux, sér. 3, t. iii, 1887, p. 346.
[2] Vergl. Anat. d. Tubifloren, Bot. Centralbl., 1892, i, pp. 199, 200 and 225.
[3] iv. Teil, Abt. 3 a, 1891, pp. 41, 42.
[4] See 'Holzstruktur,' 1885, pp. 183, 184.
[5] Org. de sécrét., Ann. sc. nat., sér. 5, t. xiv, 1872, p. 146 et seq. and pl. 10 and 13.

external glands with a long stalk, but provided with a unicellular head, or one that is bicellular owing to the presence of a vertical wall, are found in *Loeselia coccinea*, and are accompanied by others with a shorter stalk, but with a glandular head of the same structure. The glandular hairs of *Collomia linearis* have a long uniseriate stalk; they differ essentially from those just described, inasmuch as the head, which has the form of an inverted truncate cone, consists of two tiers of cells, the lower being formed by 8, the upper by 16 cells. Finally, it may be added that the leaf-teeth of the young leaf are sometimes glandular, e.g. in *Polemonium coeruleum*[1], where they contain the termination of a vascular bundle accompanied by mucilage-bearing parenchyma, while the adjacent upper epidermis includes a group of stomata.

HYDROPHYLLACEAE.

The Hydrophyllaceae share the following anatomical characters. As in the Polemoniaceae, the vascular bundles are not bicollateral. The stomata have no special subsidiary cells, but are surrounded in an irregular manner by an indefinite number of epidermal cells. The vessels of the wood have simple perforations. In *Eriodictyon glutinosum*, Benth., one of the few shrubby species, the wood-prosenchyma bears bordered pits. Where cork has been observed (*Nama*, *Eriodictyon*, and *Wigandia*), it arises superficially, immediately below the epidermis. Oxalate of lime, when present, is deposited in the form of clustered crystals. The hairy covering consists of (*a*) simple, usually unicellular, rarely uniseriate hairs, and (*b*) glandular hairs. The simple unicellular hairs are in many cases encrusted with carbonate of lime, or contain (and this sometimes applies to the surrounding cells also) cystolith-like bodies, encrusted with lime; in such cases the hairs mostly have a rigid appearance. The glandular hairs are very widely distributed and possess various types of structure. The anatomical features of the Hydrophyllaceae point to a closer relationship with the Boragineae, in which both simply collateral vascular bundles and cystolith-hairs occur, than with the Convolvulaceae, which are characterized by bicollateral vascular bundles and secretory cells.

The **leaf-structure** has hitherto been little investigated. Vesque mentions that the mesophyll is bifacial in the species investigated by him, but commonly shows a tendency towards centric structure. The latter is also the case in *Eriodictyon glutinosum*, which I have casually examined. The **stomata**, as stated above, are surrounded by an indefinite number of ordinary epidermal cells; species of *Hydrophyllum*, *Nemophila*, *Phacelia*, *Hydrolea* and *Nama* have been examined with regard to this point. The stomata are either found on both sides of the leaf (e. g. in *Hydrolea spinosa*, L.) or only on the lower surface (e. g. in *Hydrophyllum virginicum*, L., *Phacelia tanacetifolia*, Benth., &c.).

The **hairy covering** is very varied and abundant. A number of anthors, amongst others Peter, Schlepegrell, Schibler and O. Schmidt, have studied this subject, but unfortunately only in a superficial manner; they overlooked the cystolith-like deposits in the simple hairs, referred to above and described by Vesque and Radlkofer previously to the work of some of these authors, and their description of the glandular hairs is incomplete. It is therefore impossible to give an exhaustive account of the trichomes of the Hydrophyllaceae in the following description. Simple, unicellular hairs are of very wide distribution. They usually have a conical shape and sometimes a wall of considerable thickness with a verrucose surface. Such unicellular hairs occur, for example, on the leaf of *Hydrolea spinosa*, L., where they are two-celled in isolated cases, owing to the appearance of a horizontal wall. Sometimes these unicellular hairs are

[1] Reinke, Sekretionsorgane, Pringsheim Jahrb., Bd. x, 1876, p. 156.

seated on a short, multicellular pedestal, e.g. in *Phacelia Purshii, Wigandia*[1] *Kunthii* and *W. macrophylla*, according to Schlepegrell. In many cases, as stated above, they are encrusted with carbonate of lime, or contain cystolith-like bodies (according to Vesque in species of *Hydrophyllum, Nemophila*, and *Phacelia*, according to Radlkofer in *Codon Royeni*, L., *Emmenanthe penduliflora*, Benth., and *Phacelia tanacetifolia*, Benth.).

I have examined these cystolith-hairs in greater detail on the leaves of *Hydrophyllum virginicum*, L., *Phacelia tanacetifolia*, Benth., *P. congesta*, Hook., and *Nama undulatum*, H.B.K. *Hydrophyllum virginicum* has bristle-hairs, in which the wall is encrusted with lime and the lumen is filled with the same substance. *Phacelia tanacetifolia* has both unicellular hairs with calcified walls, and hairs with a bulbous swollen base, the actual hair forming, as it were, the long stalk of a cystolith, which projects convexly into the basal portion of the trichome, and almost entirely fills it. Numerous transitions are found between the hairs of the first and second type. In *Phacelia tanacetifolia* cystolith-formation is sometimes not confined to the hair, but extends to the neighbouring cells, as in certain Boragineae, e.g. *Lithospermum officinale*. In such cases the epidermal cells immediately surrounding the trichome, or even several rings of epidermal cells around its base contain calcified, cystolith-like structures. The leaves of *Nama undulatum* show cystolith-hairs of the same type as in *Phacelia tanacetifolia*; sometimes cystolith-like bodies are found in the cells adjoining these hairs, though in less abundance; *Phacelia congesta* has cystolith-hairs alone.

In *Eriodictyon glutinosum* elongated, contorted, unicellular hairs form the dense felt on the lower side of the leaf. Uniseriate, multicellular hairs appear to be more uncommon in this Order; they are stated by Peter to occur in *Tricardia, Romanzoffia* and *Ellisiophyllum*. The same author describes stellate hairs in *Hydrophyllum appendiculatum*, Michx. and strong spines (emergences) in *Codon*.

Glandular hairs are mentioned in the literature in species of *Hydrophyllum, Ellisia, Phacelia, Romanzoffia, Codon, Wigandia* and *Hydrolea*, but they are, as a rule, insufficiently described. The following description is, therefore, essentially confined to the glandular hairs on the leaves of *Hydrolea spinosa*, L., *Nama undulatum*, H. B. K., and *Eriodictyon glutinosum*, Benth., and is based on my own observations. The external glands of *Hydrolea spinosa* have a stalk of varying length and an ellipsoidal, multicellular, glandular head with horizontal and vertical division-walls; the long stalks consist of a row of cells of which the two or three basal cells are long and have thick walls, whilst the one or two succeeding cells are shorter and have thinner walls; in the shorter stalks the longer basal cells are wanting. Similar glandular hairs are described by Vesque in *Phacelia tanacetifolia*, and by Schlepegrell in *Wigandia Kunthii*. The glandular hairs of *Nama undulatum* are composed of a long stalk-cell, a short neck-cell, and a spherical glandular cell. According to Schibler, the external glands of *Hydrophyllum appendiculatum*, which likewise have a unicellular glandular head, may be classed with the preceding type. The glandular hairs of *Eriodictyon glutinosum* have quite a different structure. They are peltate glands with a unicellular stalk, and a shield consisting of four or more cells separated by vertical walls which are approximately radially arranged; the margin of the shield is slightly lobed.

Clustered crystals of **oxalate of lime** are found, for example, in the veins of the leaf of *Hydrolea spinosa, Phacelia congesta*, and *Eriodictyon glutinosum*; in the last of these species they also occur in the chambers of the elongated and transversely septate palisade-tissue and in the pith and cortex of the axis.

The **petiole** in *Wigandia caracasana* has a closed ring of wood and bast in the characteristic region, enclosing a central vascular bundle, with a few smaller

[1] The trichomes of *Wigandia urens*, which have an analogous structure, are stinging hairs (Haberlandt).

bundles on the upper side of the main system; in *Hydrophyllum canadense* we find an arc of wood and bast with two vascular bundles on each side (C. de Candolle and Petit).

The structure of the **branch** attains the greatest degree of differentiation in the shrubby *Eriodictyon glutinosum*. In this species the pith is lignified. The xylem-ring shows vessels with small lumina and simple perforations, and with bordered pits, where they are in contact with parenchyma; uniseriate medullary rays; and wood-prosenchyma with distinct bordered pits. In the pericycle there is a composite and continuous sclerenchymatous ring. The cork consists of cells with rather wide lumina and thin walls; it develops sub-epidermally (as also in species of *Nama* and *Wigandia*, according to Schlepegrell).

Regarding the stem-structure of the remaining species, which are mostly herbaceous, the following statements may be quoted from Peter and Schlepegrell. The vascular bundles, which are invariably simple and collateral, may either be separated by strips of ground tissue of varying breadth (*Hydrophyllum, Ellisia*), or be more or less intimately united to one another (*Nemophila*, Phacelieae), or lastly, they may appear as a closed ring in a transverse section of the stem (*Whitlavia, Emmenanthe, Nama*, &c.). The soft bast either forms relatively large groups (*Phacelia, Nama Lobbii*, Gray, *Codon*), or a ring (strongly developed in *Hydrophyllum, Cosmanthus, Tricardia, Nama, Wigandia*, slightly developed in *Nemophila, Nama undulatum*, H.B.K., and *N. hispidum*, Gray), or sometimes only very small groups (*Hydrolea, Romanzoffia*). In *Codon Royeni* groups of bast-fibres are found external to the soft bast (Schlepegrell). In the outer cortex a distinct starch-sheath is frequently present; in *Ellisia Torreyi*, Gray and *E. chrysanthemifolia*, Benth. the middle zone of the outer cortex consists of two layers of conspicuously large cells. The outer cortex is traversed by wide schizogenous air-canals in *Hydrolea*, the cells adjacent to the canals being filled with clustered crystals of oxalate of lime.

Literature: Martinet, Org. de sécrét., Ann. sc. nat., sér. 5, t. xiv, 1872, p. 183 and pl. 18.—C. de Candolle, Anat. comp. d. feuilles, Mém. Soc. sc. phys. et d'hist. nat. de Genève, t. xxvi, 2, 1879, p. 442.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. i, 1885, pp. 297, 298.—Haberlandt, Brenno., Sitz.-Ber. Wiener Akad., Bd. xciii, Abt. 1, 1886, p. 128 et seq. and Tab.—Schibler, Vergl. Anat. d. Borag., Diss., Bern, 1887, pp. 61, 62.—Petit, Pétiole, Mém. Soc. sc. phys. et nat. de Bordeaux, sér. 3, t. iii, 1887, p. 347 and pl. vi.—O. Schmidt, Behaar. d. Labiaten etc., Diss., Freiburg i. Br., 1888, pp. 62–4.—Radlkofer, in Sitz.-Ber. Münch. Akad. 1890, p. 123.—Schlepegrell, Vergl. Anat. d. Tubiflor., Bot. Centralbl. 1892, i, pp. 194–9.—Peter, in Natürl. Pflanzenfam., iv. Teil, Abt. 3 a, 1892, pp. 55, 56.

BORAGINEAE.

1. Review of the Anatomical Features. The following characters may be specially pointed out: the absence of bicollateral vascular bundles; the lack of a special type of stoma; the presence of simple perforations in the vessels; the occurrence of (*a*) unicellular cystolith-hairs (bristle-hairs or strigae, Fig. 127, *B–D*), in which the wall is entirely or partially calcified and the basal portion often contains a cystolith-like body, and (*b*) glandular hairs with a stalk of varying length, but always with a unicellular head (Fig. 126, *F–J*). Special internal secretory receptacles are not present. Oxalate of lime is excreted in the form of solitary and clustered crystals or as crystal-sand (the latter in *Cordia, Patagonula, Saccelium*, and *Tournefortia*). Other points to be noted in the structure of the axis are as follows: (*a*) the first formation of cork may take place at different points, either immediately below the epidermis, or in the middle of the primary cortex or in the pericycle; (*b*) the wood-prosenchyma bears bordered or simple pits; (*c*) the wood-parenchyma varies in the degree of its development; and (*d*) the outer limit of the bast is mostly formed by isolated groups of primary bast-fibres. The following anatomical features are valuable for more special diagnosis: first and foremost, the hairy covering (Figs. 126 and 127), which, however, is only known at all fully in *Cordia*[1] through Mez's

[1] Malpighian hairs have also been observed in the genus *Halgania* (see the section on structure of the leaf).

researches, cystolith-hairs of various kinds being found in this genus as well as uniseriate, malpighian and semi-malpighian, branched and glandular hairs of varied form; the appearance of independent cystoliths (species of *Cordia*, Fig. 127, *A*, and *Tournefortia*), or of cystolith-like structures in the basal portion of the cells of the hairs and occasionally also in the subsidiary cells of the hairs (species of *Cerinthe, Onosma*, &c., Fig. 127, *B–D*); the occurrence of wedges of bast in the xylem-mass in *Tournefortia hirsutissima* (according to Crüger).

2. Structure of the Leaf. In the general features of the **leaf-structure** the greatest variations occur, as might be expected. All transitions from typical centric leaves to those of bifacial structure are found, sometimes even in the same genus, as Mez has shown in the case of *Cordia*. The palisade and spongy tissues also exhibit variations. According to Mez, it is to be noted that in the genus *Cordia* the species of the section *Gerascanthus* have a palisade of several layers, whereas all the remaining species of *Cordia* with the single exception of *C. gerascanthoides*, H. B. K., exhibit a single layer of palisade-cells, some of which may be divided by horizontal walls (especially in the species of the section *Gerascanthopsis*). The cells composing the middle tissue in the centric leaves of *Lithospermum callosum*, Vahl contain little chlorophyll, while those of *Echiochilon fruticosum*, Desf. and other species have clear contents, and in those of *Trichodesma africanum*, R. Br. the contents are mucilaginous (Volkens). The structure of the smaller **veins** has only been examined in detail in *Cordia*, where they show a tendency to be vertically transcurrent above and below, or, at any rate, above. In *Heliotropium fruticosum*, L. the vascular bundles of the veins are surrounded by a sheath of parenchymatous cells with wide lumina. Sclerenchymatous fibres, running irregularly in the mesophyll and connected with the sclerenchyma of the veins, have only been recorded in *Cordia Sprucei*, Mez. The **epidermal cells** of the leaf have straight or undulated lateral walls. Neither development of hypoderm nor gelatinization of the epidermis [1] of the leaf has been observed in any member of the Order; on the other hand, papillose differentiation of the lower epidermis occurs in some species of *Cordia* (*C. ferruginea*, R. et Sch., *C. oaxacana*, A. DC., and *C. glandulosa*, Fres., belonging to the section *Varronia*). According to Strasburger and Vesque, the **stomata** belong to the Cruciferous type, but this is frequently obscured so that no special arrangement of the epidermal cells around the guard-cells is recognizable. In the case of *Cordia*, Mez states that the stomata may either lie on a level with the epidermal cells, or may be depressed (*C. subopposita*, A. DC. and *C. Rothii*, R. et Sch.), or elevated; according to the same observer, strongly elevated stomata occur, for instance, in all species of the section *Varronia*, in *C. Chamissoniana*, Steud. and *C. insignis*, Cham., and stomata borne on an elevation like a shaggy hair in *C. macrophylla*, Mill., *C. Sellowiana*, Cham., and *C. pubescens*, Willd. Similar features may well be of frequent occurrence in other members of the Order. With regard to the distribution of the stomata, we may mention that Schibler, who chiefly examined living, native species, met with them in most cases on both sides of the leaf. In the genus *Cordia* they are mostly found on the lower side only, more rarely on both surfaces of the leaf.

The **hairy covering** has very great systematic importance. Both clothing and glandular hairs occur. The characteristic clothing hairs (cf. Fig. 127, *B–D*) are unicellular, conical, bristle-hairs or strigae with a rather thick, smooth or verrucose wall; they have a cystolith-like character owing to calcification and simultaneous silicification of the tip or of the entire wall of the hair, or owing to the filling up of the lumen of the hair with carbonate of lime, or the development of a cystolith-like body in the basal portion of the hair, which is often bulbous

[1] On the other hand, according to De Bary and Frank, mucilage is found in immense quantities in the roots of the Boragineae (*Symphytum*, *Cynoglossum*); it is stated that this mucilage is not the product of metamorphosis of the cell-wall, but that it represents cell-contents.

and swollen. These hairs are the cause of the rough surface of the leaves, &c. in the Boragineae. The glandular hairs (cf. Fig. 126, *F–J*) may have a short stalk of one or a few cells, or a longer stalk consisting of more numerous cells but uniseriate; in all cases the head is unicellular but may vary in shape. In addition to these two main types, the following forms occur: simple uniseriate hairs, according to Mez in *Cordia*, and, according to C. Schmidt, in other members of the Order also (species of *Symphytum*, *Borago*, *Myosotis*, *Echium*); uni- or multicellular branched hairs, uni- or multicellular malpighian hairs, stellate hairs and 'Kropfhaare' (unicellular, semi-malpighian hairs) according to Mez in certain species of *Cordia*; also unicellular, malpighian hairs with a calcified wall, according to my own observation, in *Halgania*.

The bristle-hairs or strigae (Fig. 127, *B–D*) are conical, unicellular trichomes, which are inserted upright or obliquely on the surface of the organ; their surface is smooth, granular, or verrucose. Typically, they are thick-walled and, as stated above, cystolith-like. Their wall is impregnated with silica. The calcification either extends only to the tip or to the entire body of the hair, the lumen of the latter being in many cases occupied by cellulose-caps, between which carbonate of lime is deposited, sometimes to such an extent that the whole trichome appears to be filled with lime. The cystolith-like bodies in the base of the hair, which is often strongly swollen in a bulbous form, will be referred to below. The bristle-hairs are not uncommonly accompanied by special subsidiary cells, differing from the other epidermal cells in shape. The subsidiary cells exhibit a more typical differentiation when, as in the hair, calcification of the cell-wall occurs, or cystolith-like bodies appear, or when they project above the level of the other epidermal cells and form a kind of pedestal, bearing the hair. The internal tissue of the leaf sometimes also takes part in the formation of these pedestals (*Anchusa arvensis*). A series of unicellular hairs, which may be considered as modifications of bristle-hairs, may now be referred to. Among these are unicellular hairs, bent into the form of a hook at the apex (bracket-hairs), and stated by Schibler to occur on the calyx of *Myosotis* and on the leaf-surface of *Symphytum officinale*; and also the hairs occurring in *Cynoglossum*, *Lithospermum oleaefolium*, *Eritrichium*, and *Heliotropium*, according to Schibler, as well as in *Borago officinalis*, according to my own observation, and consisting of a small, bulbons basal portion and a very long, narrow, and thin-walled terminal portion resembling a mycelium. Other modifications of the bristle-hairs are due to a reduction in length, or a reduction of the hair-like, terminal portion. These modifications are connected with a stronger development of the cystolith-character of these hairs. In the Boragineae there is a distinct antagonism between the two tendencies to form trichomes and cystoliths respectively. In the long bristle-hairs no cystolith is present, only the wall being calcified, or even only the tip of the hair. Secondly, in slightly smaller bristle-hairs the formation of plugs of lime filling the lumina of the hairs is common. And finally, still smaller hairs contain a true cystolith in their basal portion. The smaller the body of the hair, the more typical and well-differentiated is this cystolith and, as the extreme case, the finest cystoliths are met with in epidermal cells which show no trace of hair-development. This reduction of the body of the hair and the accompanying stronger development of the cystoliths has been followed in its details by Mez in *Cordia*, and is probably to be fonnd in numerous other members of the Order. The reduction of the bristle-hairs is very marked in the leaves of *Cordia mucronata*, Fres. and the species of the two sections Crassifoliae and Tectigerae. In *C. mucronata* the hair is almost reduced to its basal portion, and scarcely projects above the level of the epidermis. In all the Tectigerae the base of the hair, which is still more depressed than in the last case, bears nothing more than warts, analogous to the structures causing the roughness of the surface of the bristle-hairs in other cases. And in the Crassifoliae one sees what appear to be independent cystoliths in correspondingly enlarged epidermal cells—which, as a matter of fact, actually occur in certain species of *Cordia* (see below)—while only an extremely small solid apiculus remains to represent the actual body of the hair.

Simple uniseriate hairs have been observed in species of *Cordia*, *Borago*, *Echium*, *Myosotis*, and *Symphytum*. In the species of *Cordia* belonging to the sections *Sebestenoides* and *Myxa*, they consist of two cells with wide lumina, viz. a short stalk-cell and a long, tubular, terminal cell. Many-celled, simple, uniseriate hairs

:ur in the species of *Cordia* belonging to the section *Eremocordia*. With such
irs we may class the branched trichomes (Fig. 126, *A–B*), observed by Mez in
rdia monoica, Roxb., and *C. ovalis*, R. Br. They are multicellular and either
nsist (*a*) of a stalk-cell with a few cells attached to it in a digitate manner, so
at the whole structure appears like a hand, or (*b*) of a row of cells, some of which
ow out laterally as branches, so that the whole trichome reminds one of the antlers
a stag. Here we may also mention the unicellular trichomes (Fig. 126, *C*), ob-
rved by Mez in an undetermined species of *Cordia* and described by him as den-
'oid hairs; they recall to some extent the appearance of certain species of *Opuntia*.

Malpighian or two-armed hairs have in the first place been recorded in *Cordia*; in
iis genus, according to Mez, they are found in the groups of species named Myxae
ıd Tectigerae, and are especially well developed in *Eremocordia*, while they are often
ss distinctly differentiated in *Sebestenoides*. The hairs in question have wide
ımina and show no trace of secretion. Well-developed, two-armed hairs are
ıentioned by Mez as occurring in *Cordia Collococca*, L., *C. Myxa*, L., *C. umbraculi-*
ra, A. DC., and *C. nitida*, Vahl. In *C. Myxa* they are unicellular; the arms are
f equal length, and are either placed horizontally, or directed upwards in the form
f a V or downwards in the form of an inverted V. In the same species hairs shaped

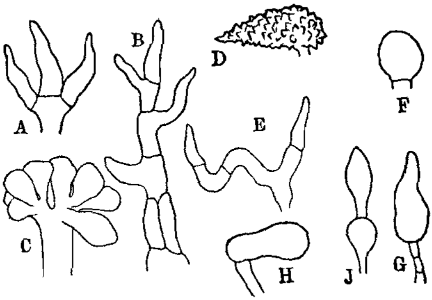

FIG. 126. Clothing and glandular hairs of the Boragineae. A–B, *Eremocordia*. C, *Cordiae Myxae*, sp. aff. D, *Cordia superba*, Cham. E, *Cordia subopposita*, A. DC. F, *Varronia*. G, *Cordia affinis*, Fres. H, *Cordia superba*, Cham. J, *Cordia glandulosa*, Fres.—After Mez.

like boot-jacks are also found, owing to the splitting of one arm. In other cases the arms are somewhat unequal, and septation of the malpighian hairs may occur (especially in the section *Eremocordia*); this septation may be restricted to the stalk (as in *C. Sebestena*, L.), so that the latter becomes uniseriate, or it also extends to the arms (Fig. 126, *E*), as in *C. subopposita*, A. DC., where, for example, accompanying two-armed hairs with a unicellular stalk and a unicellular terminal portion, others occur, in which the stalk is unicellular, whilst the terminal portion is three-celled owing to the appearance of a division-wall in each of the arms; septation also occurs in *C. grandis*, Roxb., *C. subopposita* (sphalm. '*oppositifolia*' in Mez's work), A. DC., and *C. Rothii*, Roem. et Schult., in which the elongated arms are often irregularly contorted and consist of a whole row of cells. Besides occurring in *Cordia*, the two-armed hairs are also found in the genus *Halgania* (*H. strigosa*, Schlecht.), according to a casual observation of my own. In this genus they are unicellular and possess a strongly thickened cell-wall, which, as in the bristle-hairs, is encrusted with carbonate of lime and is also covered with small knobs.

The trichomes, described by Mez as 'Kropfhaare,' and observed in species of *Cordia*, are very closely related to the two-armed hairs and might also be termed semi-malpighian or one-armed hairs (Fig. 126, *D*). They are invariably unicellular and have thick walls, which are often provided with knobs. Their terminal portion, which is seated on a short stalk, is either narrow and filiform or swollen and ovoid. These hairs are stated by Mez to occur in species belonging to the sections *Gera-*

scanthopsis, Myxae, Superbae, and Crassifoliae. The trichomes observed by the same author in some species of the section *Varronia*, e.g. *C. Radula*, Spreng., are regarded by him as a modification of the 'Kropfhaare'; they consist, so to speak, of a stalkless 'crop-hair,' the swollen end of which is inserted transversely upon a multiseriate pedestal.

According to Mez, stellate hairs occur especially in the species of *Cordia* belonging to the section *Gerascanthus*. As a rule they consist of a multiseriate pedestal of varying height crowned at the apex by the ray-cells, which have thick walls and narrow lumina, and either show a true stellate or a tufted arrangement. Outside the section *Gerascanthus*, Mez only met with stellate hairs in *C. nodosa*, Lam., *C. grandifolia*, A. DC., *C. scabrida*, Mart., *C. sericicalyx*, A. DC., and *C. multispicata*, Cham.; in these species the stellate hairs have a different structure, since they have no special supporting pedestal and their ray-cells are long and smooth. Finally the trichomes, to which *Onosma stellulatum*, Waldst. et Kit. owes its specific name, may be mentioned. These are not true stellate hairs, but are really ordinary bristles with subsidiary cells, some of which have grown out as hairs. In this way a relatively long bristle-hair appears to be surrounded by 1–2 rings of shorter trichomes, and thus the entire group acquires a stellate appearance.

The **glandular hairs** (Fig. 126, *F–J*) have been observed by C. Schmidt, Schibler, and Mez in the genera *Alkanna, Anchusa, Borago, Cordia, Echium, Heliotropium, Lithospermum, Lycopsis, Nonnea, Onosma, Patagonula, Pulmonaria*, and *Symphytum*. The stalk may be either short and formed by one or a few cells, or long and composed of a larger number of cells. The head, which is always unicellular, varies greatly in shape, and has different modes of insertion, as Mez has shown in the case of *Cordia*. It may be either spherical (sect. *Varronia*), or ellipsoidal (*C. leucocalyx*, Fres., and related species), or ovoid (*C. angustifolia*, R. et Sch.), or obovoid (*C. Aubletii*, DC.), being attached to the stalk in the normal way in all these cases, or finally, it may be ellipsoidal or biscuit-shaped, and is then attached to the stalk by one end (e.g. *C. superba*, Cham.). Glandular hairs with a uniseriate stalk, in which one or other of the stalk-cells is swollen into a capitate form, but without possessing a secretory function (*C. glandulosa*, Fres. and *C. angustifolia*, R. et Sch.), may also be specially mentioned.

The occurrence of **cystoliths** and cystolith-like structures is very characteristic of the Boragineae. Independent cystoliths, i.e. such as occur independently of hairs, have only been observed in the genera *Cordia* and *Tournefortia*, but a more extensive investigation will probably lead to their being found in other genera. Radlkofer first drew attention to the occurrence of independent cystoliths in the genus *Cordia*; according to Mez, they are found in the species of *Cordia* belonging to the sections *Gerascanthus, Gerascanthopsis*, and *Myxa*, and are thus of great systematic value for the subdivision of the genus. In the genus *Tournefortia* also, in which Mez first observed these cystoliths, they are confined to a certain number of the species, such as *T. volubilis*, L., *T. foetidissima*, L., *T. bicolor*, Sw., and *T. scabra*, Lam., whilst they are wanting e.g. in *T. gnaphalodes*, R. Br., *T. corymbosa*, Willd. and *T. floribunda*, H. B. K.

The cystoliths of *Cordia* have been more thoroughly examined by Radlkofer and Mez. In the leaf (Fig. 127, *A*) they are found only in enlarged epidermal cells, which penetrate into the mesophyll to a varying depth, but they never occur in cells actually belonging to the mesophyll. Cystolith-formation takes place more commonly in the upper epidermis of the leaf, it being exceptional for cystoliths to be present in abundance in the lower epidermis also, e.g. in *C. laevigata*, Lam. Often only quite a small portion of the surface of the cells bearing the cystoliths takes part in the formation of the leaf-surface; sometimes, as in *C. Collococca*, L. or *C. reticulata*, Vahl, they are depressed to such an extent that small pits, which can be recognized with a lens, occur above the cystolith-cells. The latter are, as a rule, isolated, groups of two or three only occurring exceptionally, e.g. on the lower side of the leaf of *C. alliodora*, Cham. and *C. Gerascanthus*, Jacq. In shape the independent cystoliths of *Cordia* are spherical or ellipsoidal bodies, which usually have a distinct stalk, and a smooth or verrucose surface, and show stratification and radial striation like the well-known cystoliths of *Ficus*. The stalk of the cystoliths varies in length—cystoliths which have no stalk are of rare occurrence (e.g. *C. glabrata*,

A. DC.). The cystoliths of *Cordia cuyabensis*, M. et Lh. and *C. alliodora*, Cham., which are situated above the veins of the leaf, are distinguished by their special form, recalling that of the well-known cystoliths of *Pilea* ; the cells containing them have a correspondingly elongated shape. Radlkofer makes the following remarks concerning the chemical reactions of the cystoliths of *Cordia*. The cystoliths are either calcified or non-calcified ; in the former case they are doubly refractive, when considerable quantities of lime are present. Cystoliths with or without lime may occur side by side in the same leaf, e.g. in *C. Gerascanthus*, Jacq. The stalk proves to be silicified, e.g. in the species just named. The portion central to the layers of stratification, and attached to the stalk, and more rarely the outer layers also, give cellulose-reactions with iodine and sulphuric acid after decalcification.

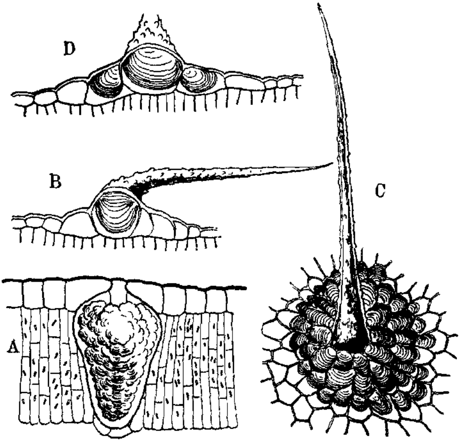

FIG. 127. *A*, Portion of a transverse section of a leaf of *Cordia Gerascanthus*, Jacq., with a cystolith-cell. B–D, Cystolith-like structures in the hairs and adjacent subsidiary cells in *Lithospermum officinale*, L.—Original.

The **cystolith-like structures** (Fig. 127, *B–D*), occurring in the basal portions of the bristle-hairs, are of much wider distribution than the independent cystoliths; they may be termed hair-cystoliths. They no doubt occur in the majority of the Boragineae, and have been examined in special detail in the genus *Cordia* by Mez. We have already referred to the antagonism existing between the well-marked differentiation of the hair, and the full development of a large cystolith. The hair-cystoliths never have a distinct stalk; they are either situated on the lateral wall of the usually bulbous base of the bristle-hair, or they are attached to the terminal portion of the hair; this is the case in those trichomes in which the terminal portion has become solid by the development of cellulose-caps and by calcification ; the cystolith-like body then projects convexly into the basal portion and often almost completely fills it. In most cases only a single cystolith-like structure is found in each hair, rarely more, as occasionally seen in *Cordia pubescens*, Willd. or *C. mirabiliflora*, A. DC., according to Mez; in the latter case the cystolith-bodies sometimes (*C. abyssinica*, R. Br.) coalesce to form a lobed mass.

In many cases the development of cystoliths is not confined to the trichomes, but extends to a larger or smaller group of neighbouring epidermal cells. In this way structures originate which are even visible to the naked eye and project as small knobs or small scales. De Bary first described these cystolith-like structures and mentions their occurrence in species of *Cerinthe, Onosma, Echium, Lithospermum* (Fig. 127, *C–D*) and *Anchusa* ; to these, according to more recent observations, we must add species of *Cordia, Caccinia, Pulmonaria* and *Lycopsis*, and no doubt many other genera. In the case in question, the base of the bristle-hair often (as in *Cerinthe*) shows rudimentary development; it is sunk in the epidermis and surrounded by one or by several concentric series of epidermal cells, which are distinguished by the fact that the whole surface of the wall directed towards the hair is provided with a cystolith-like, calcified thickening ; this projects like a hump, and fills one-half, two-thirds, or occasionally almost the whole of the lumen in the cells in question. Sometimes the epidermal cells lying nearest to the hair have only calcified walls, and it is the outer series of cells alone that contain cystolith-like bodies. A special case, observed by Mez, in *C. Sebestena*, L., is noteworthy. Here the outermost series of cells in the small knob connected with the hair is surrounded by epidermal cells, which are provided with quite small, cystolith-like bodies on the walls facing the hair and the group of cystolith-cells surrounding it; several of these bodies occur in each cell, and together they form an entire ring round the hair with its group of cystolith-containing subsidiary cells. Mez observed similar small cystoliths independently of the hairs in some species of *Cordia* (e.g. *C. sylvestris*, Fres.), in groups of 2–5, or rarely more, the cystoliths occurring singly in the corners of ordinary adjacent epidermal cells of the leaf.

In connexion with the cystoliths and cystolith-like structures it may be added that several of the forms described above may occasionally occur in the same organ of the same species. In the systematic use of the various forms a certain amount of discretion must be employed in their determination, as is sufficiently shown by Mez's treatise on the genus *Cordia*.

Oxalate of lime is present in the form of relatively small solitary crystals, small acicular crystals, clustered crystals and crystal-sand. According to Mez, all these forms are found in the genus *Cordia*. In species of *Ehretia* and in *Rhabdia viminea*, Dalz. Mez only met with clustered crystals in the tissue of the leaf. Crystal-sand [1], besides occurring in the genus *Cordia*, has been observed by me in *Patagonula*, by Radlkofer in *Saccelium* and by Mez in *Tournefortia*. The occurrence of sacs containing crystal-sand in the tissue of the Anacahuit-wood, which is derived from *Cordia Boissieri*, is interesting (Vogl, Höhnel).

The structure of the **petiole** has been investigated by Petit in species of *Anchusa, Borago, Cynoglossum, Heliotropium* and *Symphytum*, as well as in *Cordia Sebestana* and *Patagonula americana*. In the first-named genera the fibro-vascular system in the characteristic region either forms an arc of isolated vascular bundles (of which the median one is usually strongly developed), or (in *Heliotropium europaeum*) a simple arc of wood and bast; on the other hand, in the two woody species of *Cordia* and *Patagonula* referred to, there is in the same region a ring of vascular bundles, on the upper side of which two additional pairs of bundles are situated in a symmetrical lateral position.

3. Structure of the Axis. The **vascular bundles** are throughout of simple, collateral structure. Vesque erroneously attributed bicollateral structure to *Borago officinalis, Symphytum* and *Nonnea* ; he is right in describing the same structure in *Grabowskia boerhaaviaefolia*, Schlecht., which must, however, be referred to the Solanaceae in accordance with the view of modern systematists and also with its anatomical features.

[1] Kohl's statement (*Kalksalze*, p. 35), that all investigated genera of the Boragineae possess crystal-sand, is incorrect and requires considerable restriction.

The following facts are known regarding the structure of the **wood**. *This* tissue forms a connected ring in most members of the Order, even in the majority[1] of the herbaceous genera (according to Schibler). The medullary rays of the wood are narrow, though occasionally of some little breadth in *Cordia* and *Patagonula*, where they may be four cells broad; no medullary rays are present in the herbaceous members of the tribes Borageae and Ehretieae examined by Schibler. The arrangement of the vessels and the size of their lumina vary (maximum diameter = ·045 mm. in *Lithospermum fruticosum*, L., ·093 mm. in *Ehretia serrata*, Roxb.). The perforations of the vessels are generally simple; special forms have been observed in *Cordia Myxa*, L., viz. isolated, reticulate perforations (Prael, Pomrencke), and in the narrower vessels of *Lithospermum fruticosum*, perforated bordered pits with broadly elliptical openings, which cross one another. Spiral thickening is found in the narrower vessels of *Ehretia serrata* and *Lithospermum fruticosum*; in the last-named species it also occurs in the prosenchyma with bordered pits. The wood-parenchyma is, as a rule, scantily developed; in *Ehretia serrata* it forms tangential bands in the wood. The wood-prosenchyma bears simple pits in *Cordia* and *Patagonula*; in the other cases (species of *Tournefortia, Lithospermum, Ehretia, Heliotropium, Echiochilon*) it is provided with bordered pits.

The **pith** is commonly composed of unlignified cells. At the outer limit of the **bast** isolated groups of hard bast are usually present, but may be absent. In the latter case especially a distinct starch-sheath is developed (Schibler). In the genus *Cordia* a stratification of the secondary bast by means of groups of bast-fibres has been demonstrated by Mez. According to Mez, Schibler and Schlepegrell, the cork either originates subepidermally (*Cordia, Tournefortia*), or in a layer in the middle of the primary cortex (*Heliotropium peruvianum*), or in the pericycle (*Echium candicans*). The cork-cells may either have thin walls (*Tournefortia cymosa*) or some of them may be strongly thickened (*Cordia ulmifolia, Patagonula americana*).

Anomalous structure of the axis is only known in the case of *Tournefortia hirsutissima*, from Crüger's researches. The xylem-mass of this species has deep furrows, which are filled with bast-tissue. *Tournefortia laevigata* has normal structure, according to H. Schenck.

Literature: Crüger, in Bot. Zeit. 1851, p. 468 and Tab. vii.—Frank, Schleime, Pringsheim Jahrb., Bd. v, 1866–7, pp. 181–3 and Tab. xvi.—Strasburger, Spaltöffn., Pringsheim Jahrb., Bd. v, 1866–7, p. 323.—Rauter, Trichomgeb., Denkschr. Wiener Akad. 1871, pp. 22, 23 and Tab. vi, vii.—Delbrouck, Pflanzenstach., Hanstein, Bot. Abh., Bd. ii, 1875, p. 39 et seq.—Vesque, in Ann. sc. nat., sér. 6, t. ii, 1875, p. 141.—Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 57 and 353.—De Bary, Vergl. Anat., 1877.—K. Richter, Cystolith., Sitz.-Ber. Wiener Akad. 1877, sep. copy, 34 pp. and 2 Tab.—Höhnel, in Sitz.-Ber. Wiener Akad., Bd. lxxxiv, Abt. 1, 1881, p. 599.—Petersen, Bicollat. Gefässb., Engler, Bot. Jahrb., Bd. iii, 1882, p. 385.—H. Schenck, Wandverdick., Diss., Bonn, 1884, p. 11 etc.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. i, 1885, pp. 294–7.—Solereder, Holzstr., 1885, pp. 184–6.—O. Bachmann, Schild., Flora 1885, sep. copy, pp. 24, 25.—Lohrer, Wurzel, Wigand, Bot. Hefte, ii, 1887, p. 35 et seq.—Schibler, Anat. d. Bl. u. St. der B., Diss., Bern, 1887, 64 pp.—Petit, Pétiole, Mém. Soc. sc. phys. et nat. de Bordeaux, sér. 3, t. iii, 1887, pp. 360, 361 and pl. vi.—Volkens, Aegypt.-arab. Wüste, 1887, pp. 131–3 and Tab. viii, x and xiv.—C. Schmidt, Behaar. d. Labiaten u. B., Diss., Freiburg, 1888, pp. 53–61 (superficial work, *not* even taking count of the calcification of the hairs).—Prael, in Pringsheim Jahrb., Bd. xix, 1888, p. 48 and Tab. i.—Kohl, in Bot. Centralbl. 1889, i, pp. 2, 3, and Kalksalze etc., 1889, p. 142.—Petit, Pétiole, Act. Soc. Linn. de Bordeaux, t. 43, 1889, p. 30 and pl. i.—Radlkofer, in Sitz.-Ber. Münch. Akad. 1890, p. 118 et seq.—Mez, Morph. u. anat. Stud. über die Gr. d. Cordieen, Engler, Bot. Jahrb., Bd. xii, 1890, pp. 526–88 and Tab. iv–v.—Schlepegrell, Anat. d. Tubifloren, Bot. Centralbl. 1892, i, pp. 230 and 257 et seq.—Gürke, in Natürl. Pflanzenfam., iv. Teil, Abt. 3, 1893, pp. 73, 74.—H. Schenck, Anat. d. Lianen, 1893, pp. 211, 212.—Herbst, Markstr., Bot. Centralbl. 1894, i, pp. 357, 358.—Virchow, Blattzähne, Arch. d. Pharm. 1896, sep. copy, pp. 36 and 56.—Warming, Halofyt Stud., K. Danske Vid. Selsk. Skr. 1897, pp. 189, 209 and 219.

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[1] In *Symphytum officinale* and *Pulmonaria officinalis* the vascular bundles are separated by unlignified tissue (Schlepegrell).

CONVOLVULACEAE [1].

1. REVIEW OF THE ANATOMICAL FEATURES. A whole series of anatomical features characterizes this Order in an excellent manner; the most important of these are: the bicollateral nature of the vascular bundles (exception: *Humbertia*); the occurrence of secretory cells (isolated and in rows) or (in *Dichondra*) of elements resembling laticiferous vessels, both frequently having milky contents; the frequent appearance of small acicular crystals of oxalate of lime in the mesophyll; the prevalence of a stomatal type with two subsidiary cells placed parallel to the pore of the guard-cells; and the uniform structure of the clothing hairs (Fig. 129, *A–D, F–G*). The latter almost invariably consist of two cells, viz. (*a*) a suberized stalk-cell, seated on an epidermal cell or on a group of epidermal cells, and (*b*) a terminal cell of variable shape. In some cases the terminal cell is simple, its base being inserted in an upright position (simple clothing hairs), or in an oblique or horizontal direction (one-armed or semi-malpighain hairs) on the stalk-cell; in other cases, which are of very wide occurrence in the Order, the terminal cell is two-armed (two-armed hairs), and in still other cases, which are only found in the true species of *Erycibe* and *Jacquemontia*, it is three- or many-armed (branched and star-shaped hairs). In addition to the clothing hairs, glandular hairs (Fig. 129, *C, J, K*) are very widely distributed; these mostly have a short, unicellular stalk and a variously shaped head, which is divided by vertical walls only, or by horizontal walls only, or by both. Protective shaggy hairs (sometimes differentiated like a stellate or tufted hair) and glandular shaggy hairs occur in rare cases. Noteworthy features in the structure of the axis are as follows: the vessels have lumina of very variable size and simple perforations; the wood-prosenchyma bears bordered pits; the medullary rays of the wood are narrow; the development of cork takes place superficially; the outer limit of the bast is commonly occupied by isolated bundles of bast-fibres. Oxalate of lime is found in the form of clustered and ordinary solitary crystals. The anomalies in the structure of the branch consist in: (*a*) the appearance of successive rings of growth (in species of *Argyreia, Calonyction, Erycibe, Hewittia* (?), *Ipomoea, Maripa, Merremia, Porana,* and *Rivea*, see Fig. 130); (*b*) the occurrence of interxylary phloem (in *Ipomoea versicolor*, Meissn.); (*c*) a cleavage of the xylem-mass (in *Merremia umbellata*, Hallier f and *Erycibe malaccensis*, Clarke); (*d*) the occurrence of ordinary, medullary, vascular bundles (in species of *Rivea*); and (*e*) of bands of wood on the outer side of the intraxylary phloem (in species of *Argyreia, Erycibe, Evolvulus, Hewittia, Neuropeltis, Prevostea* and *Stictocardia*). Very complicated anomalies appear in the fleshy, thickened roots of certain members of the Order (see Fig. 131). As special anatomical features, which are only of value in the diagnosis of small taxonomic groups, the papillose differentiation of the lower epidermis of the leaf (species of *Maripa*) and the peculiar groups of cells in the mesophyll of certain species of *Ipomoea* (Fig. 128) may be mentioned.

[1] As reference will repeatedly be made in the following description to Hallier's classification of the Convolvulaceae it will be best to quote it at once: A. Psiloconiae: I. Cuscuteae: *Cuscuta*; II. Wilsonieae: *Wilsonia*; III. Dichondreae: *Hygrocharis, Dichondra, Falkia*; IV. Dicranostyleae: *Evolvulus, Hildebrandtia, Cladostigma, Cressa, Stylisma, Seddera, Prevostea, Bonamia, Neuropeltis, Dicranostyles, Lysiostyles*; V. Poraneae: *Rapona, Porana, Cardiochlamys*; VI. Erycibeae: *Maripa, Erycibe, Humbertia*; VII. Convolvuleae: *Jacquemontia, Aniseia, Convolvulus, Calystegia, Hewittia, Polymeria, Merremia, Operculina*. B. Echinoconiae: VIII. Ipomoeeae: *Lepistemon, Ipomoea, Calonyction, Quamoclit*; IX. Argyreieae: *Rivea, Argyreia, Blinkworthia*. Hallier leaves the Cuscuteae amongst the Convolvulaceae, whilst he excludes the Nolaneae. The anatomical features of these two groups are treated separately below in appendices to the Order. The nomenclature of the species on the whole follows that of Hallier; but in order to prevent confusion Schlepegrell's statements have been left in his own nomenclature, which is based on that of Peter.

2. Structure of the Leaf. The anatomy of the leaf has been examined in detail by H. Hallier.

The **epidermal cells** may have straight or strongly undulated lateral walls. The cuticle is mostly thin and sometimes striated. The outer walls of the epidermal cells are in many cases arched convexly outwards, especially at the margin of the leaf, where this feature may sometimes be more pronounced, amounting to the formation of papillae (*Calystegia Tuguriorum*, R. Br., *Ipomoea Batatas*, Lam., &c.). The formation of papillae on the leaf-surface occurs in *Maripa glabra*, Choisy and *M. cayennensis*, Meissn., where it is confined to the cells adjoining the stomata, and in *M. longifolia*, Sagot, in which all the cells of the lower epidermis are papillose. In most cases the epidermis consists of a single layer. The formation of a true **hypoderm** has not been observed in any member of the Order; on the other hand, the epidermis occasionally becomes locally two-layered by the appearance of horizontal division-walls; this is the case in the upper epidermis of *Ipomoea peltata*, Choisy, *Lysiostyles*, *Maripa densiflora*, Benth. and *Erycibe laevigata*, Wall., and in both upper and lower epidermis of *Dicranostyles scandens*, Benth. Gelatinization of the epidermis of the leaf has not been observed in any member of the Order. The **stomata** are very commonly developed on both surfaces of the leaf, in the case of centric as well as bifacial leaves; in leaves with well-marked, bifacial structure they are often only present in small numbers on the upper side, and are confined to the neighbourhood of the veins. The stomata are mostly accompanied by two subsidiary cells, placed parallel to the pore; three neighbouring cells, sometimes differentiated like subsidiary cells, are found in many species of *Breweria*, *Evolvulus*, and *Erycibe*, and in *Hildebrandtia* and *Cladostigma*; four neighbouring cells occur in species of the genera just named, and in species of *Convolvulus* and *Merremia*; a still larger number of neighbouring cells is found in *Ipomoea peltata*, Choisy. The guard-cells either lie on a level with the epidermis or project above it, or they may be depressed, as for example in *Ipomoea peltata*, Choisy and *Maripa passifloroides*, Spruce, where they are deeply sunk.

The **leaf-structure** varies from centric to bifacial; within certain limits is of systematic value. In many of the low-growing genera (*Breweria*, *Evolvulus*, *Convolvulus*), and also in *Hildebrandtia*, *Cladostigma*, *Cressa*, *Stylisma* and *Seddera*, centric leaf-structure is a constant feature, whilst in other genera and especially in the taller forms th s type of structure is exceptional; in the smallest forms, which are provided with leathery leaves, it does not occur. Bifacial structure of the leaf is most marked, owing to the presence of spongy tissue with large and abundant intercellular spaces, in the leathery leaves of *Humbertia*, *Erycibe*, *Maripa*, *Neuropeltis*, *Dicranostyles*, *Lysiostyles*, and of some species of *Breweria*. In other cases the spongy tissue is less typically developed. In *Aniseia uniflora*, Choisy and *Cardiochlamys* the cells of the spongy tissue have a femur-like form, and are vertically placed. The leaf-structure of *Ipomoea pedata*, Hochst. et Steud. and of *Wilsonia* requires special mention. In the species of *Ipomoea* a hollow cylinder of palisade-parenchyma surrounds a mass of large-celled medullary tissue, in which the system of veins is situated. A tissue of the same nature is found in the fleshy leaves of the species of *Wilsonia*, viz. on the upper side in the imbricate leaflets of *W. humilis*, R. Br., and within the centrically arranged palisade-tissue in the cylindrical leaves of *W. Backhousii*, Hook. f. and the flat leaves of *W. rotundifolia*, Hook. The collenchymatous differentiation of the spongy tissue in species of *Jacquemontia*, e.g. *J. lactescens*, Seem., may also be noted. The **veins** in many species contain a layer of hard bast, which adjoins the system of vascular bundles in the form of a closed sheath or of separate arcs; according to Hallier, these strands of hard bast have a systematic value for special diagnosis which should not be underestimated.

Sclerenchymatous fibres from these sheaths of hard bast occasionally penetrate more or less abundantly into the mesophyll, and not uncommonly extend as far as the epidermis and spread out beneath it on both sides of the leaf (*Dicranostyles*, very many species of *Erycibe* ; *Humbertia*, *Lysiostyles*, many species of *Maripa* ; *Prevostea ferruginea*, Choisy). They mostly have thick walls and narrow lumina. The hard bast-fibres (and also the fibres of the wood-prosenchyma) in *Erycibe micrantha*, Hallier fil. and *Prevostea spectabilis*, Meissn. are distinguished by curious excavations in their walls. Finally it may be mentioned that collenchymatous tissue often takes part in the formation of the veins, and that the vascular system of the latter is commonly surrounded by a parenchymatous sheath.

Peculiar groups of cells arranged in a row, and distinguished by their small size from the neighbouring cells, have been observed by Hallier in the palisade and spongy tissue of certain Ipomoeeae (*Ipomoea angulata*, Mart., *I. asarifolia*, R. et Sch., *I. bahiensis*, Willd. Fig. 128, *I. bonariensis*, Hook., *I. commutata*, R. et Sch., *I. cyanantha*, Griseb., *I. fastigiata*, Sweet, *I. jamaicensis*, Don, *I. involucrata*, Beauv., *I. Morelii*, Duch. et Walp., *I. pes tigridis*, L., *I. pubescens*, Lam., *I. punctata*, E. Mey., *I. rhynchorhiza*, Dalz., *I. squamosa*, Choisy, *Quamoclit coccinea*, Mch.) In the palisade-tissue these groups of cells have a palisade-like shape; in the spongy tissue they form horizontal rows, the component cells being sometimes (*Ipomoea bahiensis*, *I. Morelii*) quite peculiar in their shape. Vogl had previously observed similar groups of cells in the primary cortex of *Convolvulus arvensis*, L., and, according to Hallier, a tendency to form these groups is also manifested in other tissues of the leaf, e.g. in the integumental tissue (in *Dicranostyles scandens*, Benth. and less distinctly in *Maripa glabra*, Choisy, *M. erecta*, Mey. and *M. cayennensis*, Meissn.), in the elongated, tubular, secretory cells of the palisade-tissue to be described in detail below (in *Ipomoea rosea*, Choisy), and in the parenchymatous sheaths of the veins (in *I. bahiensis*).

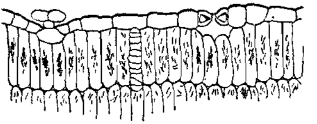

FIG. 128. Transverse section through the upper half of the leaf of *Ipomoea bahiensis*, Herb. Willd., with the characteristic 'rows of spicular cells.'—Original.

In the following description we shall deal in order with the mode of excretion of oxalate of lime, the characteristic secretory cells [1], and the hairy covering, both the leaf and axis being taken into account.

Oxalate of lime is excreted in the form of (*a*) small acicular crystals, (*b*) small crystals of varied shape, (*c*) ordinary, large, solitary crystals, and, (*d*) clustered crystals. The acicular crystals are found in the leaf in almost all cases, and are specially abundant in *Evolvulus* and *Convolvulus* ; those in the palisade-tissue are often long and form aggregates resembling bundles of raphides. The clustered crystals occur in the mesophyll and in the veins of the leaf ; in the axis especially in the chambered crystal-fibres of the bast. In the mesophyll large clustered crystals sometimes fill correspondingly large idioblasts (*Trichantha* ; *Bonamia Balansae*, Hallier f. ; species of *Calystegia*, e. g. *C. sepium*, Aut. ; *Lepistemon flavescens*, Bl. ; species of *Ipomoea*, e. g. *I. lachnosperma*, Choisy, *I. sulphurea*, Hochst., &c.), whilst small clustered crystals occupy the compartments of septate palisade-cells (*I. Aitoni*, Bot. reg., *I. involucrata*, Beauv.,

[1] Schlepegrell's statement (loc. cit., p. 353) that the resin of the Convolvulaceae occurs in 'canals,' is incorrect, and so is Volkens' statement with regard to 'oil-canals with distinct epithelium' in the neighbourhood of the vascular bundles of the veins in *Convolvulus lanatus*, Vahl, and also Harz's (Samenkunde, p. 752) reference to glands in the seedling of *C. arvensis*, similar to those of *Gossypium* (which are secretory cavities).

I. pes tigridis, L., *I. pilosa*, Sw., *I. Wightii*, Choisy); in the mesophyll of *I. setifera*, Poir the clustered crystals, which are of no great size, give rise to pellucid dots. Ordinary large solitary crystals appear, for example, in the veins of species of *Rapona* and most species of *Maripa*[1].

The internal secretory system of the Convolvulaceae consists of: (*a*) the widely distributed secretory cells, commonly possessing milky contents[2], which in herbarium-material may be colourless, yellow or brown, and are readily soluble in alcohol; in many cases (species of *Stylisma, Breweria, Convolvulus*) they give rise to transparent dots or lines in the leaf; and (*b*) laticiferous vessels, which only occur in the genus *Dichondra*.

The **secretory cells** appear in two forms: (*a*) as long rows of cells[3] running in the pith and primary cortex and sometimes also in the phloem of the axis, and in the parenchymatous sheaths of the veins of the leaf; and (*b*) as isolated secretory cells occurring in the mesophyll and in the pith and primary cortex. Commonly, both forms are developed side by side in the same plant. With regard to the general distribution of the secretory cells, Hallier mentions that in certain species they may be found in all (vegetative and reproductive) parts, but that this is not the case in other species. According to him, the occurrence of secretory cells in the cotyledons is of the greatest importance from a systematic point of view. For, when the secretory cells were not to be found in the leaf and the remaining portions of the mature plant (species of *Humbertia, Erycibe, Maripa, Dicranostyles, Neuropeltis, Cladostigma, Seddera, Breweria, Prevostea, Evolvulus, Porana, Cardiochlamys, Convolvulus, Argyreia*), they could almost always (excepting *Seddera*) be shown to be present[4] in the seedling.

The rows of secretory cells may be recognized in a transverse section of the leaf and axis by their wide lumina, their contents, and their suberized cell-walls, and frequently also by the nature of the surrounding elements, which are differentiated like subsidiary cells. In the leaf they can usually be traced from the leaf-base into the finest veins (in the Echinoconieae and most Convolvuleae); in some cases, however, they are confined to short tracts of the veins, while in other cases (*Porana volubilis*, Burm., *Prevostea glabra*, Choisy, *Seddera evolvuloides*, Wight) they are wanting. Rows of secretory cells, running independently of the vascular bundles of the veins and usually also parallel to the midrib, have been met with in *Aniseia*, s. str., and all the Jacquemontieae (excepting *Ipomoea luxurians*, Moric. and *I. hirtiflora*, Mart. et Gal.). Regarding the mode of development of the rows of secretory cells, see Czapek; the only statement we need quote from his investigations is that the rows of secretory cells sometimes undergo degeneration in mature portions of the plant, owing to the cells losing their contents and becoming compressed; in such cases their presence can only be detected by the microchemical behaviour of their suberized membranes.

The solitary secretory cells are likewise easily recognized by their suberized membranes, their contents, and their shape. The latter differs from that of the neighbouring cells, and in the leaf is dependent on the nature of the surrounding tissue. In the palisade-tissue the secretory cells only differ from the remaining elements in length or breadth; they either have a narrow, tubular shape

[1] We may mention here that Zimmermann observed crystalloids in the chloroplasts of the mesophyll in *Convolvulus tricolor*; regarding crystalloids in the nuclei of the Convolvulaceae, see also Borzi, loc. cit.

[2] Hallier observed starch in the secretory cells of *Ipomoea purpurea*, Lam.

[3] The statements of Trécul, Vogl and Schmitz that elements in these rows of secretory cells fuse together, are denied by De Bary and Czapek.

[4] In the following cases, in which only incomplete material was available, it has hitherto been impossible to demonstrate secretory cells: *Humbertia*, *Maripa longifolia*, Seg., *Cladostigma*, *Evolvulus niveus*, Mart., *Porana paniculata*, Roxb. and *P. grandiflora*, Wall., *Cardiochlamys* and *Convolvulus chondrilloides*, Boiss.

becoming enlarged like a flask when they happen to penetrate into the spongy tissue (*Quamoclit*), or are merely wide and sac-like (*Breweria, Ipomoea Spruceana*, Benth.). Those situated near the limit between the pal sade and spongy tissues are, for the most part, elongated horizontally; they are often very long and are sometimes (*Ipomoea Nil*, Roth, *I. jamaicensis*, Don, &c.) produced above into short arms. At the limit of palisade and spongy tissue we find secretory cells of the following types: (*a*) spherical or ellipsoidal (*I. suffulta*, Don, *I. filipes*, Benth., &c.); (*b*) much elongated horizontally (*Evolvulus*), sometimes with short protrusions, and occurring, either singly or several in a row, in each mesh of the vascular system; (*c*) long and branched (*Bonamia Balansae*, Hallier f., *B. venulosa*, Meissn., *Stylisma, Dichondra repens*, Forst., *Falkia*).

With regard to the distribution of the secretory cells (in rows or singly) in the leaf Hallier mentions the following facts. In the Erycibeae sensu emend. and the Poraneae, the mode of occurrence of the secretory cells varies; the Dicranostyleae, Dichondreae, and *Wilsonia*, for the most part, have only solitary secretory cells; the Convolvuleae sens. str. and Echinoconieae invariably have rows of secretory cells, usually limited to the veins of the leaf (only *Jacquemontia* and *Aniseia*, sens. str. having others running freely in the mesophyll), whilst the Convolvuleae and Ipomoceae usually have solitary secretory cells as well.

The **laticiferous vessels**, observed by Czapek in *Dichondra*, are tubular latex-receptacles, devoid of transverse septa and having thick walls which are not suberized. They exhibit no anastomoses, but have been shown to originate by fusion. In the stem they are found in the primary cortex; in the leaf they are not confined to the veins, but traverse the mesophyll, terminating near the margin of the leaf.

Radlkofer first drew attention to the most important forms of **hairy covering** and to the systematic value of this feature, which was subsequently examined by Schlepegrell and Hallier, by the former in the axis, by the latter mainly in the leaf. The trichomes may be divided into three groups, viz. clothing, glandular and shaggy hairs; and the latter may be subdivided into clothing and glandular shaggy hairs.

The **clothing hairs** almost invariably[1] consist of two cells. They are composed of a short stalk-cell, seated on a single epidermal cell or group of cells, and of a terminal cell of variable shape. In some cases the terminal cell is simple and unbranched and inserted vertically or obliquely on the stalk-cell (Fig. 129, *A*); according to Hallier, this type is found in all Echinoconieae, in *Operculina, Merremia, Shutereia, Calystegia, Polymeria, Aniseia*, some species of *Jacquemontia*, many species of *Convolvulus, Porana volubilis*, Burm., and *Dufourea* (?) *velutina*, Mart. et Gal. In other cases the terminal cell has two arms, which are generally of equal length (Fig. 129, *B–C*); according to Hallier, such hairs occur in *Cardiochlamys, Rapona, Prevostea, Breweria, Stylisma, Seddera, Cressa, Cladostigma, Hildebrandtia, Neuropeltis, Dicranostyles, Lysiostyles, Maripa, Humbertia, Wilsonia*; some species of *Convolvulus, Jacquemontia* and *Porana*; almost all *Evolvuli*; several species of *Erycibe*; and the Dichondreae, incl. *Hygrocharis*. The shape of the two-armed, terminal cell varies, and is not quite devoid of systematic importance. Hairs with straight, horizontally placed arms (Fig. 129, *B*), which may have either thin walls (*Convolvulus, Neuropeltis, Dicranostyles*) or thick walls and narrow lumina (*Hildebrandtia, Evolvulus*) are not very frequent; the arms are far more commonly directed upwards in the shape of a V (Fig. 129, *C*). In other cases the terminal cell participates in the formation of the stalk of the hair and is

[1] In *Ipomoea cairica, I. rosea*, Choisy, *Jacquemontia menispermoides*, Choisy and *J. Martii*, Choisy, a row of stalk-cells has been observed, in the first case by Schlepegrell, in the others by Hallier.

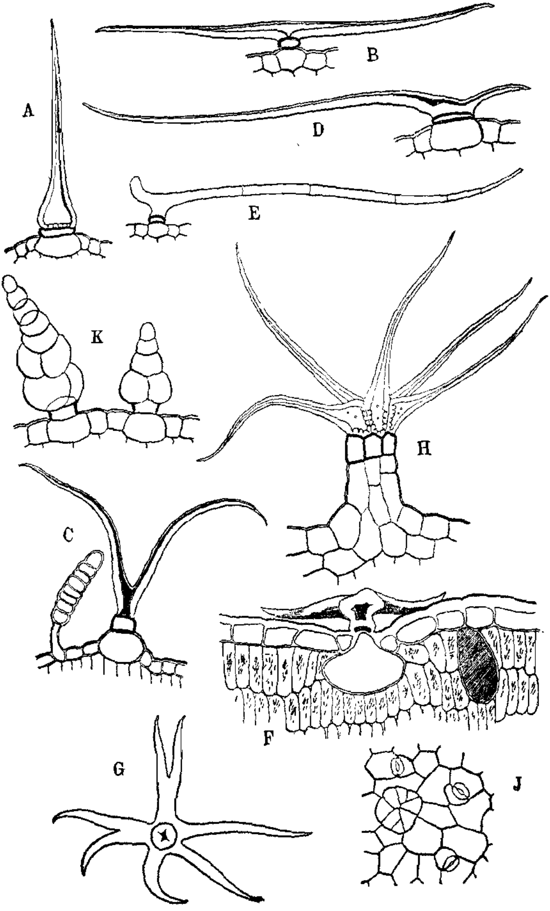

FIG. 129. Forms of hairs found in the Convolvulaceae: A, *Ipomoea fulvicaulis*, Hallier f.; B, *Dichondra repens*, Forst.; C, *Bonamia ferruginea*, Hallier f.; D, *Evolvulus villosus*, R. et P.; E, *Maripa passifloroides*, Spruce (corolla); F–G, *Jacquemontia (Convolvulus) jamaicensis*, Hallier f.; H, *Ipomoea contorquens*, Choisy; J, *Maripa passifloroides*, Spruce; K, *Cardiochlamys madagascariensis*, Oliv.—Original.

then either Y-shaped (*Cardiochlamys, Evolvulus, Falkia*) or T-shaped (*Duperreya, Lysiostyles*). By reduction of one of the arms, trichomes with two very unequal arms, or only a single arm (Fig. 129, *D*) result; these sometimes accompany hairs with equal arms, e. g. in *Porana grandiflora*, Wall. The occurrence of septa in the long arm of hairs of this type in species of *Maripa*, e. g. *M. passifloroides*, Spruce (Fig. 129, *E*) is specially noteworthy. Finally, the terminal cell may possess many arms (Fig. 129, *F–G*). According to Hallier, these hairs only occur in species of *Erycibe* and *Jacquemontia*. The number of arms varies from three to a large number.

The stalk-cell of the clothing hairs has suberized walls, and is either shortly cylindrical (in the trichomes having a simple or two-armed terminal cell) or bell-shaped, with the convex arched surface on the upper side (in the trichomes with a branched terminal cell); in many species of *Convolvulus* and *Evolvulus*, e. g. *C. natalensis*, Bernh., and *E. hirsutus*, Lam., the elliptical division-wall between the stalk and terminal cell is provided with peculiar pitting, recalling the appearance of a scalariform perforation with few bars, arranged parallel to the short axis of the ellipse. The epidermal cells bearing the hairs are, in many cases, distinguished by their considerable size. In place of a single basal cell the hairs sometimes have several, lying side by side (*Argyreia rubicunda*, Choisy, *Lysiostyles*, species of *Neuropeltis* and *Dicranostyles*). The further appearance of horizontal walls in such a group of cells leads to the formation of a multicellular pedestal (*Ipomoea pandurata*, Mey., *I. tenuirostris*, Choisy, *Cardiochlamys*). In this way we obtain a transition to the clothing shaggy hairs of *Ipomoea pentaphylla*, Jacq., *I. rhynchorhiza*, Dalz., *I. cissoides*, Griseb., and *Skinneria caespitosa*, Choisy; in these hairs several stalk-cells, situated side by side in one plane, and followed by a simple terminal cell, are seated on a multicellular pedestal. In *Ipomoea albiflora*, Moric., several terminal cells appear instead of one, while in *I. tomentosa*, Meissn., *I. contorquens*, Choisy (Fig. 129, *H*), *I. Davenporti*, F. v. Müll., *I. bonariensis*, Hook., *I. lachnosperma*, Hochst. and *Convolvulus malvaceus*, Oliv., we find numerous terminal cells, which are arranged in a stellate or tufted manner.

The **glandular hairs** are widely distributed. According to Hallier, they only appear to be wanting in *Humbertia, Wilsonia*, and some species of *Convolvulus*. The stalk is usually short and unicellular, rarely (*Jacquemontia hirsuta*, Choisy and *J. erecta*, Choisy) uniseriate; it is in most cases situated on an epidermal cell, of varying shape, the lower end of which often penetrates into the internal tissue. The structure of the head is variable. In some cases it is divided by vertical walls only, and is flat or spherical, consisting either of two (*Erycibe* sp.), four (*Erycibe laevigata*, Wall., *Neuropeltis, Dicranostyles densa*, Spruce, Dichondreae incl. *Hygrocharis, Bonamia madagascariensis*, Thouars, *Cardiochlamys*, most species of *Porana*, some *Evolvuli, Convolvulus occidentalis*, Gray, *Aniseia* sens. str., *Ipomoea luxurians*, Moric. and *I. hirtiflora*, Mart. et Gal.) or more numerous cells (many Ipomoeeae and Argyreieae, *Maripa*, Fig. 129, *J. Neuropeltis*). In other cases horizontal walls predominate in the glandular heads (Fig. 129, *C* and *K*). To this type belong (*a*) the pear-shaped or ellipsoidal glandular heads which are divided solely by horizontal walls and are found in species of *Erycibe, Dicranostyles densa*, Spruce, *Prevostea glabra*, Choisy and *P. umbellata*, Choisy, *Cladostigma*; (*b*) the elongated heads of *Prevostea ferruginea*, Choisy, which are also divided by horizontal walls only, and resemble a segmented worm; and (*c*) the spherical or ellipsoidal glandular heads, which have both horizontal and vertical walls and occur in *Stylisma, Seddera, Cressa, Hildebrandtia, Lysiostyles*, most species of *Breweria* and *Evolvulus*, many species of *Convolvulus, Jacquemontia serrata*, Meissn., and *J. micrantha*, Don. Both forms of glandular hairs sometimes occur together, but more commonly those of the second type are found alone (especially in *Evolvulus*

and *Breweria*). In *Maripa* and *Erycibe paniculata*, Roxb. the glandular hairs are very deeply sunk in the surface of the leaf. Hallier demonstrated a curious arrangement, serving for the protection of the glandular hairs and probably also for the accumulation of masses of secretion, in all true species of *Exogonium* and in many of the allied species of *Ipomoea*; this consists in the occurrence of very large numbers of glandular hairs in more or less closed grooves on the lower side of the leaf, the grooves mostly running on both sides of the larger veins, more rarely (*Ipomoea Blanchetii*, Choisy) at some distance from them. Volkens mentions the presence of external glands excreting salt in *Cressa cretica*, L., whilst Hallier describes similar glands with calcareous excretion in certain closely allied species of *Ipomoea*, belonging to the section *Pharbitis*.

Glandular shaggy hairs have been observed on the calyx and vegetative organs in three species only, viz. *Ipomoea cissoides*, Griseb., *I. albiflora*, Moric. and *I. ericoides*, Meissn., but they occur at the base of the stamens in the majority of the Convolvulaceae; they consist of a multicellular pedestal and a large, ellipsoidal, glandular cell.

The structure of the extra-floral nectaries, occurring at the base of the leaf or on the petiole in species of *Calonyction* and *Ipomoea*, has been examined chiefly by Poulsen (see also Ewart) in *Batatas edulis* and *B. glaberrima* (= *Ipomoea paniculata*, according to Hallier) and by me in *I. cicatricosa*, Bak. In the last species the nectaries constitute two lateral grooves, situated in the upper part of the petiole; they consist of numerous peltate, glandular hairs, which are only distinguished from the ordinary peltate glands of the leaf by the far greater number of rays forming the shield, and the considerable height of the ray-cells, which at some points are divided by walls parallel to the surface of the shield. The nectaries occurring at the base of the leaf in *Batatas edulis* and *Ipomoea paniculata* are flask-shaped depressions which have a narrow mouth and sometimes exhibit a number of subsidiary excavations; their wall is covered with crowded peltate glands, distinguished as in the previous case by having a shield composed of numerous cells.

The **petiole** has only been investigated in *Convolvulus* and *Ipomoea* by Petit; it contains a bicollateral arc of wood and bast in the characteristic region, and 1 or 2 isolated vascular bundles adjoin each end of the arc.

3. Structure of the Axis. Almost all investigated members of the Order[1] possess **intraxylary phloem**; *Humboldtia* is the only known exception. The intraxylary phloem is mostly developed in the form of isolated groups of soft bast; it contains chambered fibres with clustered crystals, and rows of secretory cells; its internal margin is commonly strengthened by bast-fibres, rarely (*Porana paniculata*, *Neuropeltis racemosa*, according to Schlepegrell) by arcs of sclerosed parenchyma. In some species strips of wood, containing vessels, are developed at the outer margin of the internal soft bast; these together with the intraxylary phloem may be interpreted as medullary, inversely orientated, vascular bundles. These bundles sometimes (*Erycibe malaccensis*, Clarke; Loher, Manila) grow in thickness to a considerable extent by means of strips of cambium, which are situated between the wood and bast. They have been observed in the following cases: by me in *Erycibe ferruginosa*, Grift., *E. malaccensis*, Clarke, and *Neuropeltis racemosa*, Wall.; by Schlepegrell in *Erycibe glaucescens*, *E. paniculata*, *Neuropeltis Maingayi*, *Prevostea Soyauxii*, *Evolvulus villosus*, *Argyreia tiliaefolia* (= *Stictocardia tiliaefolia*, Hallier f.) and *A. hancorniaefolia*; by Chodat and Roulet in *Hewittia Barbeyana* n. sp. (according to Hallier identical with *H. bicolor*, Wight).

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[1] A detailed enumeration of the material investigated is omitted owing to the complicated synonymy; the works of Vesque, Petersen, Solereder, Schlepegrell and Hallier should be referred to.

With regard to the structure of the **wood**, an examination of species of *Convolvulus, Ipomoea, Erycibe, Neuropeltis, Cressa,* and *Wilsonia* led me to point out the following features as being specially characteristic: the narrow medullary rays, the simple perforations of the vessels and the wood-prosenchyma bearing bordered pits; Hallier also met with these features in *Humbertia, Lysiostyles, Dicranostyles,* and *Maripa.* Schlepegrell likewise mentions narrow medullary rays and simple vessel-perforations as occurring quite generally in the abundant material investigated by him. The following statements may be added from my 'Holzstruktur.' The diameter of the vessels varies greatly, (maximum = ·21 mm. in *Ipomoea corymbosa,* Roth, a liane, and ·01 mm. in *Wilsonia humilis,* R. Br.). The bordered pits on the walls of the vessels are mostly of considerable size; where the wall is in contact with parenchyma, it bears bordered pits and transitional forms to simple pits. The wood-parenchyma is sometimes developed in considerable abundance.

The **pith** usually consists of unlignified, more rarely of lignified cells. Stone-cells commonly occur in this tissue and sometimes constitute transverse partitions (*Maripa cayennensis,* Meissn., according to Hallier), or they may form a sclerotic cylinder, separating the internal pith from the intraxylary phloem (*Neuropeltis ovata,* Wall. and *N. racemosa,* Wall.). Medullary vascular bundles have been observed in *Rivea speciosa* and *R. cymosa* (Schlepegrell).

The structure of the **cortex** has been examined especially by Schlepegrell. The cork generally arises in the epidermis or in the subepidermal cell-layer; according to Chodat and Roulet, its development is quite irregular in *Hewittia bicolor,* Wight, for here the phellogen appears in the epidermis at some points while in the rest of its course it traverses the outer cortex, the pericycle, and still more deeply seated tissues. The cork-cells either have thin walls (species of *Rivea, Ipomoea, Breweria, Seddera, Wilsonia*) or some of them are sclerosed on the outer (*Erycibe paniculata*) or inner (*Maripa glabra*) tangential wall; in other cases again they are sclerosed on all sides (*Erycibe glaucescens, Operculina Schwackei, Maripa passifloroides*). The primary cortex commonly contains collenchyma, and in species with reduced leaves assimilatory tissue. In the pericycle one meets with bundles of bast-fibres, which sometimes (*Erycibe paniculata, Porana paniculata*) unite to form a ring. These bast-fibres may either have thin walls and wide lumina (in most species of *Ipomoea*), or thick walls and narrow lumina (*Rivea speciosa*); in the latter case they are often characterized by a well-marked stratification of their walls (*Prevostea ferruginea*), or they are septate (*Neuropeltis Maingayi*). Bast-fibres have not been observed in the secondary bast, but sclerotic parenchyma occurs (*Humbertia,* according to Hallier, *Dicranostyles scandens,* according to Schlepegrell). Regarding crystals and secretory organs, see above, p. 564 et seq.

Certain members of the Order exhibit **anomalies in the structure of the axis,** which may, in some cases, be detected in herbarium-material. The following features are not to be regarded as true anomalies: (*a*) the complete or partial absence of lignification in the secondary xylem found in certain cases (*Ipomoea brachypoda, I. pterygocaulos, Breweria Roxburghii, Convolvulus nitidus, Exogonium arenarium,* according to Schlepegrell); (*b*) the restriction in many Convolvulaceous lianes of the secondary xylem-vessels to two or three tracts in the transverse section of the wood, leading to a very unequal differentiation of the xylem-mass, since it is more strongly developed at these points; and (*c*) a slight furrowing of the xylem-mass, e. g. in *Merremia glabra* (Choisy), Hallier f., according to H. Schenck. In addition to these cases, the following true anomalies have been observed: (*a*) the appearance of successive rings of growth, (*b*) interxylary phloem, and (*c*) cleavage of the xylem-mass. Successive rings of growth are known to occur in several genera; thus they were observed by Jussieu in

Convolvulus malabaricus, by Witte in *Ipomoea violacea** [1], by Krüger in *Porana volubilis** (Fig. 130) and *Argyreia capitata**, by Schöber in *Calonyction speciosum*, Choisy, by me, as described in my 'Holzstruktur,' in *Rivea corymbosa*, Hallier f. (= *Convolvulus domingensis*) and *Ipomoea jamaicensis*, Don, by H. Schenck in *Merremia umbellata* (Mey.), Hallier f., and recently by me in *Argyreia hirsuta*, Wight et Arn. (Wight n. 1953 in Herb. Monac.) and *Maripa* sp. (Rusby and Squires n. 92, Orinoco); that is to say, they are found in species of *Argyreia*, *Calonyction*, *Ipomoea*, *Maripa*, *Merremia*, *Porana*, and *Rivea*. With regard to the mode of origin of these rings of growth, it may be mentioned that the first of the secondary meristematic rings appears at the outer margin of the bast and internally to the bast-fibres of the pericycle. According to more recent observations, extrafascicular formation of secondary bundles of wood and bast, which are not, however, arranged in regular circles, is found in the older portions of the stem of *Erycibe malaccensis*, Clarke (collected by Loher); in this case it is accompanied by a cleavage of the normal, primary vascular ring, the outer margin of which has lobed furrows, and by the marked growth in thickness of the inversely orientated medullary bundles (see above). Extrafascicular formation of secondary bundles apparently also takes place in *Hewittia bicolor*, Wight, according to Chodat and Roulet. The anomaly of successive rings of growth will doubtless be found in other woody genera as well; but it is certain that all the woody Convolvulaceae do not show this kind of anomaly. According to H. Schenck, an axis of *Convolvulus canariensis* (Mus. Berol.) about 2 cm. thick, and branches of *C. pentanthus* and *Ipomoea pentaphylla* (sent by Goebel) 7 mm. in thickness, proved to have normal structure. Scott met with interxylary phloem in the hypocotyl and lowest internodes of *Ipomoea versicolor*. In this plant the xylem contains a large amount of unlignified parenchyma enclosing small bundles of sieve-tubes. These are either given off on the inner side of the cambium simultaneously with the parenchyma or differentiate subsequently from the latter. According to H. Schenck, cleavage of the xylem-mass in consequence of subsequent dilatation and division is also found in *Merremia umbellata*, accompanying the first anomaly.

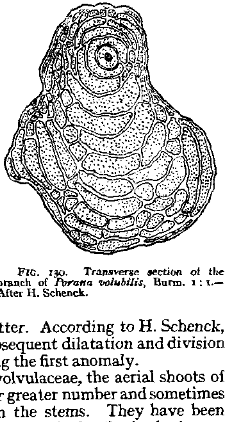

FIG. 130. Transverse section of the branch of *Porana volubilis*, Burm. 1 : 1.—After H. Schenck.

In the fleshy, thickened roots of many Convolvulaceae, the aerial shoots of which die down annually, we find anomalies in far greater number and sometimes of a much more complicated type than those in the stems. They have been thoroughly examined by Schmitz and consist, to express it shortly, in the formation of new vascular bundles in the wood and bast of the root.

In the young stage, roots, which become anomalous as they increase in age, show a xylem-mass having a large amount of unlignified parenchyma and surrounded by soft bast, which likewise contains abundant parenchyma. Secondary formations originate in the xylem by the division of the unlignified parenchymatous cells surrounding the groups of primary vessels. In some cases the root remains in this condition. In others, e.g. *Convolvulus Scammonium* (Fig. 131), a true cambial ring is formed round each group of vessels; this gives off wood internally and bast externally, so that the xylem-mass breaks up into a number of concentric fibrovascular strands. The same process is repeated once more in these secondary strands,

[1] In those species which are marked with an *, the anomaly has been confirmed by H. Schenck.

and thus a characteristic appearance of the transverse section of the root originates, as has long been known to be the case in old specimens of 'Radix Scammoniae.'

In the cases so far referred to, the appearance of the secondary meristem stands in relation to groups of vessels. In other cases, rings or strips of cambium appear independently of the vessels in the unlignified parenchyma of the wood or bast, or of both; these cambial layers produce wood on one side (usually on that towards the centre of the root) and phloem externally. A curious modification of this type is present in Tubera Jalapae, the tuberous roots of *Ipomoea purga*. In this case narrow bands of cambium are found in great numbers in the transverse section of the largely parenchymatous xylem of the original (primary) fibro-vascular system; towards the periphery of each xylem-group the bands become tangential in position, and finally they unite to form a cambial ring, which is situated within the primary cambial ring, and forms wood on the inside and bast on the outside. If continued growth in thickness takes place, several further secondary cambial zones of a similar kind

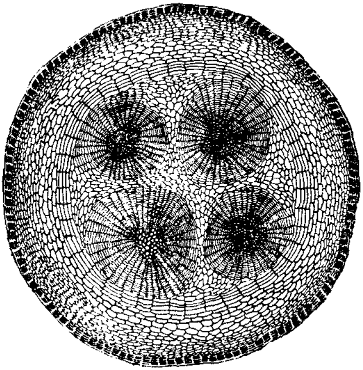

FIG. 131. Transverse section through a root of *Convolvulus Scammonium*, at a stage in which cleavage of the xylem-mass into four portions, and the development of a cambial ring around each of them, have taken place. —After Dutailly.

may develop, always originating in the youngest layers of the xylem, belonging to the primary fibro-vascular system; these cambia, however, give off bast internally and wood externally. In the xylem of these secondary rings of growth, further cambial rings appear, which are concentric with the primary and secondary rings, and, as in the primary ring, produce wood internally and bast externally. The transverse section of the root thus shows concentric cambial rings, some of which develop wood internally and phloem externally, others phloem internally and wood externally.

Similar secondary formations sometimes also appear in the very parenchymatous phloem, as in *Ipomoea Turpethum*. In this plant fibro-vascular strands arise in the phloem by cell-division; these strands consist of a central mass of wood with peripheral phloem, and grow in thickness by means of a cambium situated between the two. The root of *Ipomoea Turpethum*, moreover, shows subsequent formation of fibro-vascular strands in the xylem-mass also, and for a time they grow normally in thickness. As in the xylem, the meristems appearing secondarily in the phloem are often band-shaped; these may coalesce to form a secondary cambial ring, which after forming wood internally and bast externally for some time, ceases to be active whilst a second cambial ring appears external to the ring of growth produced by the first, and gives rise to a new ring of growth, and so on; the result is that the root shows the anomaly of successive rings of growth, and this also occurs in the stem

as described above. An anomaly of a similar nature to that just described, although of a rather more complicated type, is shown by 'Radix Jalapae Tampicensis'; in this case two successive cambial rings appear in the phloem developing in centrifugal order; they produce rings of growth, which have their xylem and phloem normally orientated; but subsequently a further ring of growth arises internally to that first formed, and gives off xylem externally and phloem internally. In the case last mentioned, as in *Ipomoea Turpethum*, formation of fibro-vascular tissue may also take place in the original xylem of the root. When this is the case, very complicated structures often result in a transverse section of the root, as in the drugs of commerce passing under the names of 'Radix Mechoacannae' and 'Stipites Jalapae'; such structures cannot be elucidated without a study of their development.

APPENDIX: 1. Cuscuteae.

A brief description will now be given of the anatomy of the Cuscuteae, which are parasitic and poor in chlorophyll, and are universally classed with the Convolvulaceae. A character very essential as supporting their association with the Convolvulaceae is the occurrence of resin-cells[1] (see Hallier, loc. cit., p. 540); whilst the following important features are in favour of their separation from that Order: in the single case (*Cuscuta monogyna*, Vahl), in which a true ring of vascular bundles occurs, the latter are not bicollateral but of the simple collateral type; glandular hairs (except for glandular shaggy hairs, similar in structure to those of the Convolvulaceae, and occurring on the scales in the tube of the corolla of *Cuscuta*, see Hallier, loc. cit., p. 540) are not present; and lastly, the clothing hairs do not resemble the trichomes of the Convolvulaceae, but are simple and consist of one or two cells, according to Radlkofer. Stomata are only to be found on the mature plant and in small numbers (Uloth).

The following facts regarding the anatomy of the **axis** may be mentioned on the authority of L. Koch. The fibro-vascular system shows three different degrees of development. The first is found in *Cuscuta Kotschyana*, Boiss. and *C. brevistyla*, A. Br., which exhibit a single concentric vascular bundle in the centre of the axis. The second occurs in the following species: *C. Epilinum*, Weihe. *C. arabica*, Fres., *C. halophyla*, Fries, *C. Epithymum*, L., *C. europaea*, L., *C. chilensis*, 'Nutt.', *C. Gronovii*, Willd., *C. rostrata*, Shuttlw., *C. africana*, Willd., and *C. americana*, L. These plants possess a number of groups of vessels, each of which is accompanied by a strand of soft bast of variable size; the groups are rather irregularly distributed near the centre of the stem. Occasionally one can apparently distinguish an annular arrangement of these fibro-vascular strands, and also a pith and interfascicular tissue (*C. Epilinum*, *C. africana*, *C. americana*); but, as in the other cases, the strands together with the apparent pith and interfascicular tissue develop from a single procambial strand. The groups of vessels and the accompanying phloem-strands, taken as a whole, form only a single axile, vascular bundle. *C. monogyna*, Vahl, alone has a true, dicotyledonous type of structure in its stem, viz. a vascular ring surrounding a true pith and consisting of 12–20 bundles, united by slightly thickened interfascicular tissue; these bundles grow in thickness by means of a cambium, and their phloem is supported by a few bast-fibres. Actual perforations are not present in the division-walls of the vessels. In *C. Epilinum* and *C. monogyna* these walls either bear a single large pit, which is simple and closed, or numerous smaller pits, which are likewise probably not perforated, or combinations of one large and several smaller pits, all of which are closed.

2. Nolaneae.

The Nolaneae, which form a tribe of the Convolvulaceae in Bentham and Hooker's work, are rightly excluded from this Order by Hallier. Endomorphic as

[1] The relation between the secretory elements (termed 'laticiferous vessels' by L. Koch) in the stem of *C. Epilinum*, *C. Epithymum*, *C. europaea*, *C. chilensis*, *C. Gronovii* (resin-canals! (?) also in this species), *C. rostrata* and *C. monogyna*, and the secretory cells still remains to be investigated. Similarly the long laticiferous tubes of *Cuscuta*, mentioned by Solms-Laubach (loc. cit., p. 575) as resembling bast-fibres and terminating in a blunt point, require re-examination.

well as exomorphic characters indicate that the Nolaneae are closely related to the Solanaceae; they were, moreover, referred to that Order by various earlier authors. The Nolaneae, like the Convolvulaceae and Solanaceae, have intraxylary soft bast; the trichomes are comparable to those of the Solanaceae, but not to those of the Convolvulaceae; oxalate of lime is excreted in the form of crystal sand [1], which only occurs in the Solanaceae; and finally the resin-cells [2] characteristic of the Convolvulaceae are wanting in the Nolaneae.

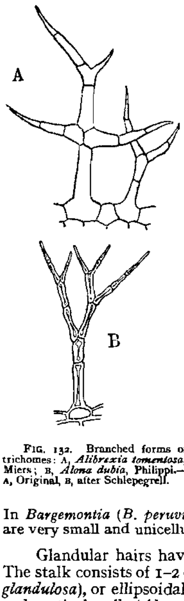

FIG. 132. Branched forms of trichomes: A, *Alibrexia tomentosa*, Miers; B, *Alona dubia*, Philippi.—A, Original, B, after Schlepegrell.

The vascular system of the **axis** is bicollateral in structure in all four genera. The internal phloem forms groups at the margin of the pith; they are occasionally (*Dolia salsoloides*) supported by groups of bast-fibres on the side facing the pith, and are sometimes situated at some distance from the xylem-ring. Isolated groups of hard bast are found in the pericycle; in *Alona* and *Nolana* these groups may be strongly developed in the radial direction. The cork arises subepidermally.

The **hairy covering** consists of clothing and glandular hairs. The clothing hairs are multicellular and either simply uniseriate or dendriform (Fig. 132, *A*), or dichotomously branched (Fig. 132, *B*); in very rare cases they are simple and unicellular.

Amongst the species of *Alona*, *A. phylicifolia* and *A. floribunda* have simple uniseriate hairs, while *A. dubia* has multicellular, dichotomously branched trichomes (Fig. 132, *B*). All the species of *Nolana* examined by Schlepegrell have simple, uniseriate hairs. Within the genus *Dolia* dendriform hairs have been met with in *D. salsoloides*, *Alibrexia albescens*, and *A. tomentosa* (Fig. 132, *A*), simple, uniseriate hairs in *D. vermiculata*, *D. puberula*, and *Alibrexia brevifolia*. In *Bargemontia* (*B. peruviana*, *Haplocaria divaricata*) we find hairs, some of which are very small and unicellular, whilst others are multicellular and slightly branched.

Glandular hairs have been observed by Schlepegrell in *Alona* and *Nolana*. The stalk consists of 1–2 cells; the head is either spherical and unicellular (*Alona glandulosa*), or ellipsoidal and multicellular, owing to the presence of horizontal and vertical walls (*Alona dubia*).

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[1] Crystal-sand is mentioned by Vesque and Hallier as occurring in species of *Alona*, *Nolana*, and *Dolia*. Schlepegrell does not definitely state whether it also occurs in *Bargemontia*.

[2] Schlepegrell remarks that 'latex appears in the pith and cortex of *Nolana*.' I was unable to find secretory cells in *Nolana prostrata*, L., *N. atriplicifolia*, Hort. and *Alibrexia tomentosa*, Miers.

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SOLANACEAE [1].

1. Review of the Anatomical Features. All the members of this Order are distinguished by the possession of intraxylary soft bast, which is frequently accompanied by sclerenchymatous fibres. Special internal secretory organs are wanting. The stomata are mostly surrounded by several epidermal cells of ordinary shape; but isolated examples of the Acanthaceous type occur as well, i.e. stomata having two subsidiary cells placed transversely or obliquely to the pore (*Schwenkia*, *Melananthus*, &c.). The vessels have exclusively simple perforations; the medullary rays of the wood are generally narrow; the wood-parenchyma is scantily developed; the wood-prosenchyma bears bordered or simple pits. Isolated groups of bast-fibres are found in the pericycle, or even these are wanting. The secondary bast does not contain bast-fibres in any member of the Order. The cork develops in different positions—in the epidermis, or in the outermost cell-layer of the primary cortex, or at the outer limit of the bast. Oxalate of lime is excreted in the form of solitary or clustered crystals or of crystal sand. The latter is very widely distributed in the Order, and together with the intraxylary phloem is highly characteristic of the Solanaceae, although it does not by any means occur in all the genera. The hairy covering (Fig. 133) is often abundant and varied. Both clothing and glandular hairs are found, and the former are in most cases simple and uniseriate. Unicellular clothing hairs have only been observed in *Schizanthus*. In addition to the types mentioned, branched hairs are found in many genera, also trichomes resembling stellate hairs (*Solanum*, *Cyphomandra*, and *Dunalia*), and finally peltate hairs (species of *Solanum*). The glandular hairs are very diverse, and vary in the length of the stalk and the size of the head; the latter may consist of a single cell or of few or many variously orientated cells, and so on. The following features are also worthy of special notice: the absence of gelatinization in the epidermis of the leaf and its occurrence in the mesophyll (*Sclerophylax*); and the appearance of interxylary phloem in the wood of the root in *Atropa*, *Datura*, and *Scopolia*.

2. Structure of the Leaf. The leaf-structure has been specially examined

[1] Of the Solanaceae enumerated in Durand's index, I exclude *Retzia* (regarding this genus and the genus *Lonchostoma*, referred to the Bruniaceae by Durand, see the appendix to this Order); on the other hand *Henoonia*, *Coeloneuron* and *Melananthus* (*Schwenkia*, Benth. ex parte, *Microschwenkia*, Benth. ed. Hemsley) must be included in the Solanaceae.

by Vesque and Fedde[1]. The leaves vary in structure, but are mostly bifacial, according to Fedde. Development of hypoderm and gelatinization of the epidermis of the leaf have so far not been observed in the Order, but gelatinization of the mesophyll, similar to that shown by the species of *Vahea* (Apocynaceae), was found by Radlkofer in *Sclerophylax Lorentzianus*, O. Hoffm. The smaller **veins** of the leaf have sclerenchyma accompanying the vascular bundles in certain species only; stone-cells have been observed in the parenchyma of the veins in *Sessea stipulata*, R. et P. (Fedde). The **stomata** either occur on both sides of the leaf (e.g. in *Datura Stramonium*), or only on the lower side (as in *Atropa Belladonna*). In almost all cases they are surrounded by ordinary epidermal cells, varying in number (often three or four) and developing according to the Cruciferous type, and this is often (e.g. in species of *Jaborosa*, *Withania*, and *Solanum*, according to Vesque) still recognizable in the mature leaf. *Melananthus fasciculatus*, Solered. and all the species of *Schwenkia* which I examined, constitute an exception to this rule; for in these cases stomata, accompanied by two subsidiary cells, arranged transversely or obliquely to the pore, occur side by side with stomata of the ordinary type; according to Fedde, two similarly situated subsidiary cells are also present in *Dyssochroma longipes*, Miers and *Juanulloa membranacea*, Rusby. Depressed stomata are only mentioned as occurring in *Dyssochroma* and *Juanulloa* by Fedde. The position of the stomata in the plant described by Volkens as *Fabiana squamata*, Ph. is peculiar; they are found on the apices of wart-like elevations, so that they project far beyond the level of the resinous coating, which covers the surface of the leaf in this plant. According to Volkens, in other species of *Fabiana* (such as *F. denudata*, Miers), the branches are provided with a similar resinous coating, and also possess stomata, projecting far above the epidermal surface, and, moreover, furnished with specially long 'horns.' Certain other features of the epidermis of the leaf described by Fedde should also be mentioned, viz. the occurrence of papillose **epidermal cells** on the upper side of the leaf in *Juanulloa mexicana*, Miers and *Cestrum roseum*, H. B. K.; the presence of epidermal cells containing crystal-sand in *Salpichroa rhomboidea*, Miers, and of an excretion of wax in *Solanum glaucophyllum*.

The **hairy covering** consists of clothing and glandular hairs, and presents very diverse forms. Amongst the clothing hairs, the simple unicellular type is very rare (*Schizanthus*), whilst simple uniseriate hairs with pointed or blunt apices, and smooth or verrucose walls, are very widely distributed (*Atropa*, *Datura*, *Nicotiana*, &c.). The following special forms of uniseriate trichomes have been observed: (*a*) the hairs of *Nicandra physaloides*, Gärtn., which invariably consist of three cells (Fedde); (*b*) the trichomes of *Metternichia principis*, which are provided with a very long terminal cell (Schlepegrell); and (*c*) the trichomes of *Henoonia*, distinguished by the possession of a thickened terminal cell (Radlkofer), the remaining cells having thin walls; they are sometimes reduced to a single thin-walled hinge-cell, filled with special contents; owing to the stronger growth of this cell on the outer side (i.e. the side turned away from the part of the plant bearing the hair), the terminal cell becomes adpressed to the surface. Schlepegrell, without giving any detailed description, mentions that variously branched multicellular hairs occur in *Acnistus arborescens*, *Iochroma tubulosa*, *Poecilochroma microphylla*,

[1] Fedde's investigations, which deal with the structure of the axis as well, extend to numerous species of the following genera: *Lycopersicum*, *Solanum*, *Cyphomandra*, *Athenaea*, *Physalis*, *Chamaesaracha*, *Saracha*, *Mellissia*, *Bassovia*, *Capsicum*, *Brachistus*, *Discopodium*, *Margaranthus*, *Withania*, *Nothocestrum*, *Acnistus*, *Iochroma*, *Dunalia*, *Latua*, *Poecilochroma*, *Phrodus*, *Cacabus*, *Nicandra*, *Triguera*, *Trechonaetes*, *Jaborosa*, *Nectouxia*, *Salpichroa*, *Grabowskia*, *Lycium*, *Atropa*, *Mandragora*, *Dyssochroma*, *Solandra*, *Datura*, *Scopolia*, *Physochlaina*, *Hyoscyamus*, *Markea*, *Juanulloa*, *Cestrum*, *Goetzea*, *Sessea*, *Metternichia*, *Retzia*, *Fabiana*, *Vestia*, *Nicotiana*, *Petunia*, *Bouchetia*, *Nierembergia*, *Schizanthus*, *Salpiglossis*, *Browallia*, *Brunfelsia*, *Schwenkia*, *Duboisia*, *Anthocercis*, *Sclerophylax*.

Lycium halimifolium, *Solandra* '*Hauptii*,' *Anisodus luridus*, *Juanulloa aurantiaca*, *Cestrum laurifolium* and *Witheringia* '*spina alba*' (see also Fig. 133, *E*, *Nicotiana Tabacum*). We may add to these the branched trichomes of *Chamaesaracha Coronopus*, Gray, which are distinguished by their squat shape; the base is constituted by a large, thick, barrel-shaped epidermal cell, from which smaller lateral cells of the same shape branch off (Fedde). The candelabra-hairs

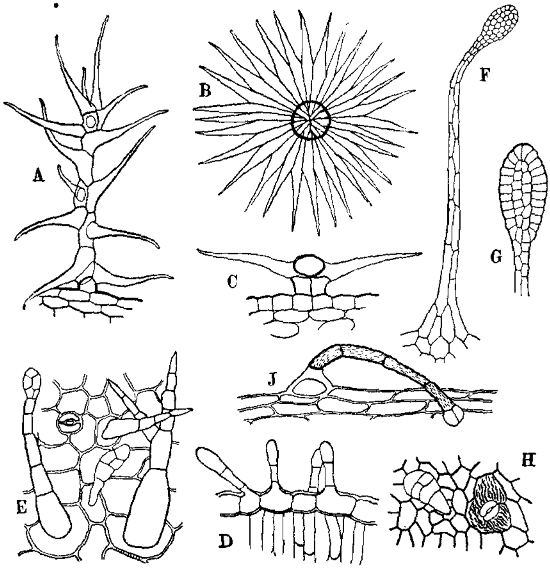

FIG. 133. Hairy covering of the Solanaceae: A, Candelabra-hair of *Sessea vestita*, Miers. B–C, Peltate hair of *Solanum argenteum*, Dun.; B, in surface-view from above, C, in section. D–J, Glandular hairs: D, *Lycium arabicum*, Schweinf.; E, Leaf-surface of the Folia Nicotianae; F–G, *Schizanthus pinnatus*, R. et P., F, showing surface-view of the glandular head, G, glandular head in longitudinal section; H, *Duboisia myoporoides*, R. Br.; J, *Melananthus fasciculatus*, Solered.—A–C and F–J Original, D, after Volkens, E, after J. Möller.

of *Sessea vestita*, Miers, may also be included here (Fig. 133, *A*, according to my own observation). Trichomes differentiated like stellate or tufted hairs are widely distributed in the species of *Solanum* (Schlepegrell, Vesque); they consist of a biseriate or multiseriate stalk and a tuft of ray-cells, of which the middle one is sometimes more strongly developed than the others. The trichomes of *Cyphomandra abutiloides* only differ from those just mentioned in the fact that some of the cells of the biseriate stalk are produced into hairs; whilst the hairs of *Dunalia* sp. are club-shaped structures, the superficial cells of which have a polygonal outline, and are occasionally developed in a hair-like form

(Schlepegrell). Peltate hairs are confined to certain species of *Solanum* (*S. argenteum*, Dun., *S. Swartzianum*, R. et Sch., *S. Vellozianum*, Dun., according to O. Bachmann, Fig. 133, *B–C*). They have a biseriate or (*S. Vellozianum*) multiseriate stalk; the numerous ray-cells start from a central cell, embedded in the middle of the shield and projecting to a varying extent above its surface.

The form of the glandular hairs is as varied as that of the clothing hairs (see Martinet, Solereder, Schlepegrell, Volkens, and the pharmacological works). Diversity is found both in the structure of the stalk, which varies in length and is unicellular or uniseriate, as well as in that of the head. Several forms commonly occur in the same species. Glandular hairs, with a short or long stalk and a spherical unicellular head, have been observed in species of *Atropa*, *Fabiana* [1], *Hyoscyamus*, *Salpiglossis* and *Sclerophylax*. Hairs of a similar structure are also found in *Melananthus*, and in the species of *Schwenkia* belonging to the sections *Cestranthus*, *Chaetochilus* and *Euschwenkia*, but in these the stalk, which is composed of a few cells, is drooping, and the head may sometimes come to consist of 2–4 cells, owing to the development of vertical, or both vertical and horizontal walls (Fig. 133, *J*). Glandular hairs with a disc-shaped head, divided by vertical walls only, occur in *Lycopersicum* and *Solanum* (composed of four cells, according to Martinet), and in the section *Brachyhelus* of the genus *Schwenkia* (with radially arranged ray-cells). In another series of external glands there is an ellipsoidal head divided by walls, which are (rarely) horizontal only, or more commonly horizontal and vertical, or irregularly arranged, the glands having short stalks in species of *Anthocercis* [2], *Atropa*, *Brunfelsia*, *Datura*, *Duboisia*, *Hyoscyamus*, *Lycopersicum*, *Nicotiana* (Fig. 133, *E*), *Physalis*, *Scopolia*, section *Cardiomeria* of *Schwenkia*, *Solanum*; long stalks in *Datura*, *Hyoscyamus*, *Nicotiana* (Fig. 133, *E*), *Salpiglossis*. In hairs of this type, if the stalk is short and graduates into the multicellular glandular head, club-shaped forms result (*Duboisia*, Fig. 133, *H*, *Brunfelsia*, section *Cardiomeria* of *Schwenkia*). The external glands (Fig. 133, *D*), described by Volkens as occurring in *Lycium arabicum*, Schweinf., require special mention; they are somewhat club-shaped structures, which consist of two cells placed one above the other, and project as papillose protuberances from the central portions of the epidermal cells. The glandular shaggy hairs of species of *Schizanthus* (Fig. 133, *F–G*) are also noteworthy; the long stalk consists of four rows of cells, surrounding a narrow intercellular canal, and the multicellular head is clothed by epidermal cells which have a polygonal outline in surface-view, and are seen to be elongated like a palisade in a longitudinal section of the head.

In addition to the clothing and glandular hairs, spines (emergences) are found in certain species of *Solanum*; they are composed of lignified tissue, the cells of which are rounded in transverse and elongated in longitudinal section.

Oxalate of lime is excreted in the form of crystal-sand, small crystals of various shapes, clustered crystals, sphaerites (in *Grabowskia boerhaaviaefolia*, Schlecht., according to Aser Poli), and ordinary, large, solitary crystals. Crystal-sand is very widely distributed; it is contained in cells of the pith, primary cortex and bast of the axis, as well as in cells of the mesophyll (very rarely also in the epidermal cells of the leaf, see above) occurring in the form of granules, which are occasionally of relatively large size and are, for the most part, distinctly tetrahedral in shape (Fig. 134). Crystal-sand has been described by different

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[1] These glandular hairs form an unusually thick, resinous crust on the leafless branches in *F. viscosa*, Hook. et Arn., *F. denudata*, Miers, and *F. Peckii*, Niederl. We may add that a similar resinous crust, which occurs in a plant described as *F. squamata*, Ph., is not due to glandular trichomes, but owes its origin to the corky tissue developed beneath the lower epidermis (i. e. outer surface) of the leaves which are here adpressed to the branches; the cells of this cork tissue are filled with the same kind of resin as that deposited superficially (Volkens).

[2] The depressed dots on the lower side of the leaf in *A. viscosa*, R. Br. are due to the external glands described above, the latter being sunk in the surface of the leaf.

authors (De Bary, Vesque, Radlkofer, Solereder, Arcangeli [1]) in certain species of the genera *Acnistus*, *Anisodus*, *Anthocercis*, *Anthotroche* (according to my own investigation of *A. pannosa*, Endl.), *Atropa*, *Brugmansia* (=*Datura*), *Cacabus* (according to a casual examination of *C. mexicanus*, Wats.), *Capsicum*, *Coeloneuron*, *Cyphomandra*, *Datura*, *Discopodium*, *Duboisia* (in *D. myoporoides*, Benth., according to a casual observation), *Goetzea*, *Henoonia*, *Jaborosa*, *Iochroma*, *Isandra* (according to a casual examination of *I. Bancroftii*, F. v. Müll.), *Lycium*, *Lycopersicum*, *Nicotiana*, *Salpichroma*, *Salpiglossis*, *Saracha*, *Sclerophylax*, *Scopolia*, *Solandra*, *Solanum*, *Vestia* and *Withania*; so far as is known it is characteristic of the genera mentioned. In the same plant, crystal-sand, even though present in the axis, is not always to be found in the leaf; for in the latter organ it is very commonly replaced by clustered crystals. Further, solitary crystals, or clustered and solitary crystals, may occur side by side with the crystal-sand in the same plant. Not uncommonly we find clustered crystals [2] embedded in crystal-sand, e.g. in *Henoonia myrtifolia*, Griseb., according to Radlkofer. The precise distribution of crystal-sand in the Solanaceae has not yet been determined, but so much is certain, that crystal-sand does not occur in all the members of the Order. Thus in *Schwenkia* and *Melananthus*, for example, oxalate of lime is always excreted in the form of clustered crystals only; the absence of crystal-sand has likewise been demonstrated by Vesque in *Fabiana* and *Nierembergia*, as well as in *Nicandra physaloides*; and in *Cestrum corymbosum*, Schlecht., *Fabiana imbricata*, Ruiz. et Pav. and *Brunfelsia Hopeana*, Benth., I was unable to find crystal-sand, at least in the axis; nor did Arcangeli meet with it in *Petunia phoenicea*. With regard to the remaining modes of excretion of oxalate of lime, it may be mentioned that rather small crystals of prismatic, cubic or octahedral shape have been observed by Fedde in the axis or leaf of certain species belonging to the genera *Atropa*, *Capsicum*, *Datura*, *Hyoscyamus*, *Iochroma*, *Saracha*, *Triguera* and *Withania*; the same author met with elongated sacs, filled with solitary tetragonal crystals in the bast of *Dunalia lycioides*, Miers.

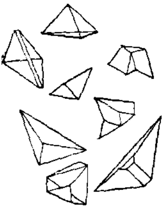

FIG. 134. Forms of crystal-sand in the Solanaceae.—After Arcangeli.

The **petiole** exhibits a uniform type of structure in the species of the genera *Atropa*, *Capsicum*, *Datura*, *Hyoscyamus*, *Lycopersicum*, *Nierembergia*, *Nicotiana*, *Physalis* and *Solanum* investigated by Petit. The fibro-vascular system in all cases consists of a bicollateral arc of wood and bast, accompanied by 1–4 smaller vascular bundles on each side of the more or less deep groove, which is present on the upper surface of the petiole.

3. STRUCTURE OF THE AXIS. An important distinctive character of the axis is to be found in the presence of **intraxylary soft bast**, which has been demonstrated by various authors (Vesque, Radlkofer, Solereder, Schlepegrell, Fedde) in numerous species of most of the genera [3]. The two exceptions, first mentioned

[1] The statements in Fedde's work are unfortunately expressed in such a general way and are so vague, that they could not be taken into account in the enumeration given above.

[2] Fedde's statement (loc. cit. p. 31) regarding the occurrence of solitary crystals embedded in crystal-sand in some members of the Order is certainly incorrect in the case of *Datura Tatula*, which is one of the species cited (see Fig. 5 in Fedde's plate, where the bodies enclosed in crystal-sand are clustered crystals).

[3] The genera are as follows (in the sequence of Durand's Index); the material investigated is only named specifically in those cases in which bicollateral structure is recorded for the first time: Trib. 1. Solaneae: *Lycopersicum*, *Solanum*, *Cyphomandra*, *Athenaea*, *Physalis*, *Chamaesaracha*, *Saracha*, *Mellissia*, *Bassovia*, *Capsicum*, *Brachistus*, *Discopodium*, *Margaranthus*, *Withania*, *Nothocestrum*, *Acnistus*, *Hebecladus*, *Iochroma*, *Dunalia*, *Latua*, *Poecilochroma*, *Phrodus*, *Cacabus*,

by Schlepegrell, viz. the genera *Retzia* and *Lonchostoma*, will be discussed in an appendix to this Order; these plants must be excluded from the Solanaceae. The internal margin of the intraxylary phloem is very commonly strengthened by sclerenchyma; the latter usually resembles bast-fibres and sometimes forms strongly developed groups. This sclerenchyma is either differentiated as a continuous ring at the margin of the pith, or in the form of isolated bundles situated in the medullary sheath; it is sometimes separated from the xylem-mass by a few layers of parenchymatous cells. Secondary growth of the intraxylary phloem by means of a cambium, situated at its outer margin, is no rare occurrence (e.g. in *Lycium barbarum*); in *Anthotroche pannosa* this cambium also produces a few vessels externally at some points. In certain cases (*Solanum tuberosum* and *S. Dulcamara*, according to De Bary, *Nicandra physaloides*, according to Petersen, *Nicotiana Tabacum*, according to De Toni, *Atropa Belladonna*, according to Hérail) medullary groups of soft bast have been observed in addition to the bast situated in the medullary sheath.

No other anomalous features in the structure of the axis are known, even in the climbing species of *Solanum* (H. Schenck). On the other hand, the wood of the root in *Datura Stramonium* and *Scopolia atropoides*, according to J. E. Weiss, and in *Atropa Belladonna*, according to Radlkofer and Beauvisage, contains interxylary phloem, which is produced by the cambium on its inner side. We may add that the concrescence, frequent in this Order, of the leaves with the shoots springing from their axils (recaulescence) is commonly also evident in the anatomical structure; a section through such points distinctly shows the limits of the vascular system of the two organs (Wettstein).

As regards the structure of the **wood**, we may mention the following facts, which are chiefly derived from Fedde's work. The vessels vary in their arrangement and the size of their lumina (maximum diameter = ·03–·09 mm.). The breadth of the medullary rays is usually small; in *Datura Metel*, L. and *D. arborea*, L., however, the rays may consist of six rows of cells (Herbst). The bordered pits on the walls of the vessels are occasionally of considerable size. Where they are in contact with parenchyma, the vessel-walls may either bear both simple (often large) and bordered pits (in the species of *Acnistus*, *Cestrum*, *Datura*, *Solandra* and *Solanum*, named in my 'Holzstruktur'), or bordered pits only (in the species of *Anthocercis*, *Brunfelsia*, *Fabiana* and *Lycium*, cited in the same work). Spiral thickening, extending to all the pitted vessels, or only to those with narrow lumina (and to the tracheids), has been observed in certain species of *Acnistus*, *Anthocercis*, *Cestrum*, *Grabowskia*, *Lycium* and *Solanum* (see Möller, my 'Holzstruktur' and Pomrencke). The perforations of the vessels are always exclusively simple. The wood-parenchyma is scantily developed. The wood-prosenchyma bears either simple or bordered pits, or transitional forms between the two (i.e. indistinct bordered pits, or simple pits accompanying others with indistinct borders [1]). The walls of the wood-prosenchyma are usually not very thick;

Nicandra, *Triguera*, *Trechonaetes*, *Himeranthus*, *Jaborosa*, *Nectouxia*, *Salpichroa*; Trib. 2. Atropeae: *Grabowskia*, *Lycium*, *Atropa*, *Mandragora*, *Dyssochroma*, *Solandra*; Trib. 3. Hyoscyameae: *Datura*, *Scopolia*, *Physochlaina*, *Hyoscyamus*; Trib. 4. Cestrineae: *Markea*, *Juanulloa*, *Cestrum*, *Goetzea*, *Sessea*, *Metternichia*, *Fabiana*, *Vestia*, *Nicotiana*; Trib. 5. Salpiglossideae: *Petunia*, *Bouchetia*, *Nierembergia*, *Leptoglossis*, *Reyesia* (*R. chilensis*, Gay, Gay, Chile, Herb. Kew), *Schizanthus*, *Salpiglossis*, *Browallia*, *Streptosolen* (*S. Jamesoni*, Miers, Herb. Kew), *Brunfelsia*, *Schwenkia*, *Duboisia*, *Anthocercis*, *Anthotroche* (*A. pannosa*, Endl., Original specimen of the Vienna Herbarium), *Sclerophylax* (also *S. spinescens*, Miers, Tweedie, Brasilia, Herb. Kew), *Isandra* (*I. Bancroftii*, F. v. Müll., Herb. Kew); finally the genera *Henoonia* and *Coeloneuron*, transferred to the Solanaceae by Radlkofer, as well as *Melananthus*.

[1] H. Schenck's statement, that 'according to Solereder' it is characteristic of the entire Order that fibrous cells containing starch form the ground-mass of the wood, is contrary to the data on this subject given in my 'Holzstruktur.' According to Fedde we find: simple pitting of the wood-prosenchyma in species of *Acnistus*, *Bassovia*, *Dunalia*, *Dyssochroma*, *Hyoscyamus*, *Iochroma*,

but the prosenchyma in species of *Brunfelsia*, *Fabiana*, *Goetzea*, *Grabowskia* and *Phrodus*, which bears bordered pits, possesses strongly thickened cell-walls. Septation of the wood-prosenchyma by means of delicate division-walls has been met with in species of *Acnistus*, *Brachistus*, *Dunalia*, *Juanulloa*, *Salpichroa* and *Solandra*.

In the structure of the **cortex** the development of the cork requires special notice. The first cork-cambium either arises in the epidermis itself (in species of *Brunfelsia*, *Datura*, *Fabiana*, *Nicandra*, *Nierembergia*, *Physalis*, *Solanum*, and *Vestia*, according to Vesque, Douliot and Fedde, and in *Duboisia*, *Melananthus* and *Schwenkia*, according to my own observations), or in the subepidermal cell-layer (in species of *Cestrum*, *Fabiana*, *Habrothamnus*, *Iochroma* and *Petunia*, according to Vesque, Möller, Douliot and Schlepegrell), or at the outer limit of the bast (in species of *Dunalia*, *Grabowskia*, *Latua*, *Lycium*, *Mandragora* and *Phrodus*, according to Douliot, Möller, Schlepegrell and Fedde).. The cork usually consists of cells with thin walls and wide lumina. Fedde has shown that, in species of *Brunfelsia*, *Markea* and *Sessea*, for example, certain of the cork-cells have thickened, inner, tangential walls, while in species of *Juanulloa*, *Phrodus*, *Sessea* and *Solandra*, the cork includes stone-cells. The outer portion of the primary cortex contains collenchyma, which sometimes (species of *Dunalia* and *Acnistus*) includes stone-cells. Part of the primary cortex is occasionally developed as a well-marked assimilatory tissue, which in *Salpiglossis sinuata* and *Leptoglossis linifolius*, for example, is differentiated like palisade-tissue, according to Schlepegrell. In the pericycle we commonly find bast-fibres, which are either isolated or united to form groups of various sizes, or a loose ring; these fibres may have thick (*Markea*, *Saracha*) or thin walls (*Lycopersicum*), and are sometimes septate (in *Salpichroa rhomboidea*, Miers and *Salpiglossis sinuata*, R. et P., according to Fedde); stone-cells occasionally occur among them (species of *Brunfelsia*). In other members of the Order, such as *Lycium halimifolium*, *Physochlaena physaloides*, *Himeranthus magellanicus*, &c., bast-fibres are entirely wanting in the pericycle. An endodermis is only in rare cases (*Browallia Jamesoni*, Benth., according to Born) developed around the pericycle. Bast-fibres have not been observed in the secondary bast, but Möller found occasional rod-cells in *Datura suaveolens*, Humb. et Bonpl. and groups of stone-cells in *Cestrum Pseudo-Quina*, Mart.

The **pith** is in many cases composed of unlignified cells, but frequently some of the cells become sclerosed (Cestrineae, species of *Brunfelsia*, *Discopodium*, *Dyssochroma*, *Duboisia*, *Salpichroa* and *Sessea*).

APPENDIX.

Retzia capensis, Thunb. and *Lonchostoma acutiflorum*, Wikstr., which have been referred to above, may now be discussed in greater detail; they are without intraxylary phloem, and must be excluded from the Solanaceae.

The two genera *Retzia* and *Lonchostoma* were regarded by Endlicher as forming an independent group, the Retzieae, and as such were appended to the Solanaceae. Miers discovered relationships between both genera and the Bruniaceae; more recently his example has been followed as regards the genus *Lonchostoma*, which by common consent has been transferred to the choripetalous Bruniaceae, an attempt being made to explain the gamopetalous corolla of *Lonchostoma* by assuming a fusion of the lower portions of the 'free' petals by means of the staminal filaments.

Nicandra, *Nicotiana*, *Physochlaena*, *Poecilochroma* and *Solanum*; transitional forms in species of *Acnistus*, *Anthocercis*, *Athenaea*, *Browallia*, *Capsicum*, *Datura*, *Fabiana*, *Nicotiana*, *Physalis*, *Salpichroa*, *Saracha*, *Schizanthus*, *Solanum* and *Triguera*; typical bordered pitting in species of *Atropa*, *Brachistus*, *Brunfelsia*, *Cacabus*, *Cestrum*, *Chamaesaracha*, *Cyphomandra*, *Discopodium*, *Duboisia*, *Goetzea*, *Grabowskia*, *Hebecladus*, *Henoonia*, *Jaborosa*, *Juanulloa*, *Latua*, *Lycium*, *Markea*, *Mellisia*, *Nierembergia*, *Nothocestrum*, *Petunia*, *Phrodus*, *Salpiglossis*, *Schwenkia*, *Sessea*, *Solandra*, *Solanum*, *Vestia* and *Withania*; and also in *Anthotroche*, *Isandra* and *Melananthus* (according to my own observation).

On the other hand, the genus *Retzia* has by general consent been left amongst the Solanaceae (being included in the Cestrineae), although it differs essentially from all other members of that Order in having whorled leaves. *Retzia* is certainly not rightly placed amongst the Solanaceae; earlier authors made unsuccessful attempts to refer this genus to the Convolvulaceae, Apocynaceae and Polemoniaceae; recently Fedde has come to the conclusion that he has found the correct position, viz. in the neighbourhood of the genus *Nuxia* among the Buddleioideae.

The following statements may be made with regard to the anatomy of the two genera in question, *Lonchostoma* being taken first. The branch of *Lonchostoma acutiflorum*, in addition to the absence of internal bast, shows the following features: (*a*) vessels with very small lumina, scalariform perforations with many bars, and bordered pits on the walls in contact with parenchyma; (*b*) narrow medullary rays; and (*c*) wood-prosenchyma with thick walls and narrow lumina, and covered with small, more or less distinct bordered pits. The bast contains solitary and clnstered crystals. The rather narrow leaves, which are adpressed to the branch, have a mesophyll showing centric structure and including cells filled with large clustered crystals; the stomata are situated on the upper side of the leaf only, and are parallel to one another, and without subsidiary cells. The hairy covering consists eutirely of long, simple, unicellular hairs with thick walls. The nature of the hairy covering and the structure of the wood are not opposed to the inclusion of *Lonchostoma* amongst the Bruniaceae.

In the monotypic genus *Retzia*, the structural features of the axis, with the exception of the absence of internal soft bast. are not quite the same as in *Lonchostoma*. The vessels, which have small lumina, are only provided with simple perforations, and bear bordered pits on the walls in contact with parenchyma. The medullary rays are narrow, as in *Lonchostoma*. The wood-prosenchyma, however, bears simple pits in *Retzia*. The thick, linear leaves have two grooves on the lower side; the stomata are confined to these grooves, the surface of which is covered with hairs throughout the life of the plant; in the young leaf hairs also spring from the epidermal cells on the upper side of the leaf, but these soon fall off. The simple hairs in question are long, unicellular trichomes with thick walls and narrow lumina; they are seated on a solid stalk-like basal portion, which constitutes a papilla on the epidermal cell from which the hair arises. When the hair falls off, this basal portion naturally remains behind. Besides the simple hairs, I have observed in *Retzia* short glandular trichomes with a unicellular stalk and a small spherical head divided by one or more vertical walls, rarely by one or two horizontal walls also. Finally a very noteworthy feature is the excretion of oxalate of lime both in the mesophyll and in the pith, in the form of small acicular crystals or small crystals of varied shape. If we consider the affinities on anatomical grounds, besides the absence of internal soft bast, the presence of elongated, simple, unicellular hairs, and the mode of excretion of oxalate of lime militate against the inclusion of the genus *Retzia* amongst the Solanaceae. The characters of the oxalate of lime, and also the structure of the wood, do not favour a close relationship between *Retzia* and the Bruniaceae.

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SCROPHULARINEAE[1].

1. Review of the Anatomical Features. Features specially characteristic of this Order are the absence of intraxylary phloem and the possession of external glands, in which the head is divided by vertical walls only. The stomata also are surrounded by three or more epidermal cells. The following points may be noted in the structure of the axis: the vessels are provided with simple perforations throughout, and bear bordered pits in contact with the parenchyma; the wood-prosenchyma, which forms the ground-mass of the wood, bears simple pits; true medullary rays are frequently absent; the pericycle shows varied differentiation; and superficial as well as internal development of cork has been observed. Excretion of oxalate of lime is rare, and takes place in the form of small, prismatic, acicular or octahedral crystals; clustered or large solitary crystals are very rare. The occurrence of carotin- and protein-crystals in the mesophyll is rather common. Idioblasts containing tannin (*Scrophularia*) are the only type of internal secretory receptacles which has been observed. The hairy covering consists of: (*a*) simple, unicellular or uniseriate trichomes, which are sometimes of the nature of cystoliths; (*b*) branched, multicellular hairs (*Verbascum*, Fig. 135, *A–B*, *Leucophyllum*, *Paulownia*); (*c*) glandular hairs, in which the stalk varies in length, and the head is unicellular, or owing to the presence of vertical walls consists of two or more cells, the hairs with a multicellular head resembling the peltate glandular hairs of the Oleaceae; and (*d*) peltate glands (Fig. 135, *C–F*) of characteristic structure, occurring in *Lathraea*, *Euphrasia* and other Rhinanthaceae, and only projecting slightly above the surface of the organ which bears them.

2. Structure of the Leaf. The leaf-structure has been examined in detail by Vesque, Chatin and E. Koch, and has been found to vary. Distinct bifacial structure is met with in some cases (e.g. *Odontites rubra*, Pers.); in others the leaves show centric structure with palisade tissue on both sides (e.g. *Scrophularia deserti*, Del.); whilst in still other cases (e.g. *Castilleja arvensis*, Ch. et Schl.) the mesophyll is entirely composed of rounded, isodiametric cells. The **epidermal cells** have various shapes in surface-view, but undulated lateral walls are especially frequent. The cuticle is thin and often striated. Usually all the walls of the epidermal cells are likewise thin; cells with thick walls, and lumina filled with tannin, only occur in desert-forms (*Linaria Haelava*, Del., *Scrophularia deserti*, Del., &c., according to Volkens). The **stomata** are either present on both sides or only on the lower side of the leaf; in the former case they may be present in equal abundance on the two sides, or may be more numerous on the lower surface. According to Vesque their development follows the Cruciferous type, but this is frequently obscured

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[1] *Lathraea*, referred by Bentham and Hooker to the Orobanchaceae, no doubt belongs to the Scrophularineae; the description of that genus is consequently included in this Order.

in the mature leaf; that is to say the stomata are surrounded by three or more epidermal cells. **Hypoderm** is mentioned as occurring in *Veronica speciosa* and *V. Lindleyana* by De Bary and Diels. Gelatinization of the epidermis of the leaf has not been observed[1]; but a red or blue colouring matter, dissolved in the cell-sap, may be present, or (still more commonly) there are chlorophyll grains in some of the epidermal cells of the leaf and stem. The tanniniferous **idioblasts** of the mesophyll of *Scrophularia deserti* are large ellipsoidal cells, attached to an epidermal cell, the lower end of which penetrates for some little distance into the mesophyll; these idioblasts extend to the middle of the leaf, where they are inserted on the ends of the veins (Volkens).

The scale-leaves of *Lathraea* and *Tozzia alpina* (which are provided with cavities), and the acicular leaves of *Hemiphragma heterophyllum*, Wall. (which has dimorphic leaves), require special mention. The scale-leaves of *Lathraea*, as is well known, have a system of hollow spaces in their interior, owing to epinastic recurving of the upper side of the leaf; these spaces are grouped like a fan, and open to the exterior by means of a narrow slit, whilst other smaller cavities branch off from them laterally. Only the surface of these scale-leaves (=morphological upper side of the leaf) is provided with stomata (Krause), whilst the epidermis of the internal cavities bears very numerous external glands (capitate and peltate). The cavities in the scale-leaves of *Tozzia* are much simpler; they are formed by the recurving of the margins and tip of the leaf, and are provided with numerous glandular hairs of the same type as in *Lathraea*; apparently stomata are not present on these leaves. The acicular leaves of *Hemiphragma*, which appear in relation to the inflorescence, likewise belong to the category of rolled-leaves, but their margins are induplicate; stomata are only present in the groove on the upper side of the leaf.

Oxalate of lime, as stated above, is generally excreted only in the form of small, prismatic, octahedral or acicular crystals. Large solitary[2] and clustered crystals have only been observed in *Paulownia imperialis*, S. et Z., the former in the pericycle, the latter in the veins of the leaf and in the petiole. According to Zimmermann, protein-crystals are usually found as constituents of the nuclei in the epidermis and mesophyll (sometimes also in the tissue of the stem) in numerous members of the Order, e.g. species of *Digitalis*, *Halleria*, *Lathraea*[3], *Linaria*, *Lophospermum*, *Melampyrum*, *Mimulus*, *Paulownia*, *Pedicularis*, *Pentstemon*, *Phygelius*, *Rhinanthus*, *Russelia*, *Scrophularia*, *Torenia* and *Veronica*; they rarely occur in the cell-sap (peltate hairs of *Gratiola officinalis*). Crystals of carotin are mentioned by Koch as occurring in the mesophyll and accompanying the vascular bundles of the veins in species of *Alonsoa*, *Antirrhinum*, *Celsia*, *Lophospermum*, *Scrophularia* and other genera; they are recognized by their solubility in alcohol, blue coloration with concentrated sulphuric acid, &c.; they appear as yellow crystals of different shapes, such as columns, plates, needles, and so on.

The following description of the **hairy covering** is based essentially on the statements of Born, Chatin, Radlkofer and Vesque. In Koch's work, and especially in that of Hoch, the description of the trichomes is too imperfect to be specially considered. The clothing hairs are generally unicellular or uniseriate trichomes, the walls of which are either smooth or provided with various cuticular thickenings. The unicellular and uniseriate hairs sometimes occur side by side in the same species. Vesque's observation that these

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[1] Koch's statement (loc. cit., pp. 16 and 40 et seq.) regarding gelatinization of the epidermis of the stem in *Linaria triornitophora*, Willd. and other species is incorrect; there is no gelatinization, but the wall of the cells shows well-marked cartilaginous thickening.

[2] I find that the 'well-developed large solitary crystals' occurring in the pith of species of *Veronica* and *Linaria*, according to Koch (loc. cit., p. 25, &c.), are only of relatively large size; they are much smaller than the solitary crystals of *Paulownia*.

[3] The Orobanchaceae contain no crystalloids (Zimmermann).

simple clothing hairs sometimes assume a cystolith-like character deserves special notice; thus the unicellular trichomes of the Euphrasieae are calcified; in *Odontites* calcified, cystolith-like structures appear to occur also in the subsidiary cells adjoining the hairs; on the lower side of the leaf of *Melampyrum arvense* we find hairs composed of two cells, of which the lower contains a cystolith-like body, attached to the division-wall common to the two cells. In *Melasma hispidum*, Benth., the trichomes, together with a group of subsidiary cells, are silicified, and give rise to small knobs on the leaf, which are visible to the naked eye. Branched multicellular trichomes have long been known to occur in *Verbascum*, and are also present[1] in *Leucophyllum* (according to Bentham and Hooker) and *Paulownia* (according to my own observation). In *Verbascum Thapsus*, L. (Fig. 135, *A–B*), the hairs in question consist of an upright, uniseriate main axis, from which whorls of from two to eight ray-cells arise at certain points; a whorl of the same type also terminates the trichome. Similar hairs are found in other species of *Verbascum*. In the floral region (*V. nigrum*, L., according to A. Weiss), and occasionally on the leaf (Virchow), these candelabra-hairs undergo reduction, thus forming stellate hairs, which, for example, may only consist of a stalk-cell, a neck-cell and three ray-cells. The trichomes of *Paulownia imperialis*, S. et Z., which are branched to a varying extent, may be regarded as representing a uniseriate hair, in which some of the cells have grown out to form rays. Glandular hairs have been shown to occur in the following genera: *Alonsoa, Antirrhinum, Bartsia, Calceolaria, Capraria, Celsia, Chelone, Collinsia, Cymbaria, Digitalis, Erinus, Euphrasia, Freylinia, Gratiola, Herpestis, Lathraea, Limosella, Linaria, Lindernia, Lophospermum, Maurandia, Mazus, Melampyrum, Mimulus, Nemesia, Odontites, Paederota, Paulownia, Pedicularis, Pentstemon, Rhinanthus, Rhynchocorys, Russelia, Schwalbea, Scoparia, Scrophularia, Torenia, Tozzia, Verbascum, Veronica, Wulfenia, Zaluzianskia.* The glandular hairs are provided with a unicellular or uniseriate stalk of varying length, and in most of the genera are distinguished by a head composed of 1–4 cells; it may be added that several forms of hair, differing in the structure of the stalk and head, may occur side by side in the same species. Glandular hairs with a short stalk and a relatively large peltate head, composed of a considerable number of cells, have been observed by Vesque in *Gratiola*, by Radlkofer in *Capraria biflora*, L., *Scoparia dulcis*, L., and *Herpestis gratioloides*, Benth., by Volkens in *Calceolaria pinifolia*, Cav., and by me in *Russelia sarmentosa*. Jacq.; in these species of *Capraria, Scoparia* and *Herpestis*, the hairs give rise to transparent dots; in *Calceolaria pinifolia* they form a coating of varnish on the leaf[2], whilst in certain species of *Melampyrum* they constitute nectarial spots on the bracts (Rathay). External glands of a peculiar kind, usually termed peltate glands in the literature, are so far known to occur in species of *Bartsia, Euphrasia* (including *Odontites*), *Lathraea, Melampyrum, Pedicularis, Rhinanthus* and *Tozzia*, and are probably widely distributed in the Rhinanthaceae. They consist of a large 'central cell,' having a broadly elliptical or almost circular shape, and, inserted upon it, a group of cells, with the same general outline; this group consists of from two to four 'lid-cells,' separated from one another by from one to three vertical walls, which, when several are present, are parallel to one another, and sometimes also to the longitudinal axis of the ellipse. In the middle of the 'lid-cells' a circular or slit-shaped opening

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[1] Koch's statement regarding the occurrence of branched hairs in *Digitalis purpurea* is incorrect.

[2] With reference to Koch's statement (loc. cit., p. 103) as to the occurrence of glandular shaggy hairs with a multiseriate stalk in '*Capraria peruviana*, L.,' I may remark that, in *C. peruviana*, Benth (= *C. biflora*, L.), I only found glandular hairs with a rather long, uniseriate stalk and a disc-shaped, multicellular head, divided by vertical walls.

may generally be seen in the cuticle; this opening owes its origin to local, subcuticular secretion, and the consequent bursting of the cuticle (Goebel). In *Lathraea* and *Tozzia* the central cell rests upon a basal portion, consisting of small cells, separated from one another by intercellular spaces; in other cases, as in *Pedicularis*, it is seated on a single basal cell. According to Goebel, the function of these peltate glands consists in the excretion of water[1]; an insect-catching function was ascribed to the glands of *Lathraea* and *Bartsia* by Kerner and Wettstein, but this has been shown to be incorrect by Scherffel

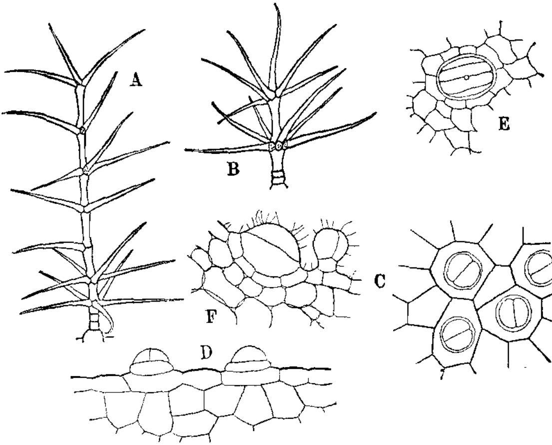

FIG. 135. A–B, Candelabra-hairs of *Verbascum Thapsus*, L. C–F, Peltate glands: C–D, *Pedicularis Sceptrum Carolinum*, L., E–F, *Lathraea squamaria*, L.—A–D, Original, E–F, after Scherffel.

and Heinricher[2]. Goebel's view is supported by the fact that spiral tracheids of the fibrovascular system extend as far as the peltate glands on the scale-leaves of *Lathraea* and *Tozzia*. Glandular excretions are also found on the leaf-teeth, e.g. in *Veronica spuria*, according to Reinke. In this species the leaf-tooth contains the termination of a vein, accompanied by an epithema containing mucilage, and there is a group of water-pores in the epidermis above.

The structure of the petiole has been investigated by Petit in species of *Calceolaria, Digitalis, Linaria, Lophospermum, Paulownia, Pentstemon, Phygelius, Scrophularia* and *Verbascum*. In the characteristic region in these species the fibrovascular system consists mainly of a variously shaped arc of wood and bast, which is almost circular and closed in *Paulownia*, or of an arc of vascular bundles, the

[1] Haberlandt describes the capitate hairs of *Lathraea* as hydathodes; they occur in great numbers side by side with the peltate hairs, and are sometimes covered with carbonate of lime.

[2] The nature of the 'protoplasmic processes' of the peltate glands, described by Kerner and Wettstein, has not yet been fully explained; Scherffel regards them as Bacteria.

xylem-groups of which are separate, whilst the bast-portions coalesce (*Maurandia antirrhinifolia, Lophospermum scandens*). Sometimes there are one or more additional bundles symmetrically arranged on each side of the groove on the upper surface, and there may also be one bundle on each side of the main system (*Calceolaria chelidonioides*), or intramedullary bundles may be present (*Paulownia imperialis*).

3. STRUCTURE OF THE AXIS. The structure of the axis has been examined especially by Chatin, Born, E. Koch and myself. Our knowledge is scanty regarding the development of the cork. Born remarks that in *Leucophyllum ambiguum*, Humb. et Bonpl., internal development of cork takes place, the phellogen appearing on the inner side of the bundles of primary hard bast; Möller found that in *Paulownia imperialis*, S. et Z., the cell-layer, situated immediately beneath the epidermis, becomes the cork-cambium, and gives rise to cork consisting of cells with thin walls and wide lumina. Collenchyma is either entirely wanting beneath the epidermis (as in *Freylinia*, *Halleria*, and other genera) or (as is generally the case in this Order) the outermost cell-layer of the cortex alone shows a slight collenchymatous differentiation. In projecting portions of the stem, when strands of collenchyma occur, they are in general only weakly developed; they are rarely strongly differentiated (e.g. in *Scoparia dulcis*, L.), and they then recall those of the Labiatae. On the other hand, according to Born, on whose account this description of the structural features of the stem is mainly based, subepidermal ribs of sclerenchymatous fibres are found in *Russelia sarmentosa*, Jacq., *Lindernia pyxidaria*, All., *Vandellia hirsuta*, Ham., *V. crustacea*, Benth., and *Bonnaya brachiata*, Link et Otto; in *Russelia sarmentosa* there are mostly six of these ribs, in the remaining species four. E. Koch observed the same feature in *Torenia Fournieri*, but he only met with isolated, subepidermal, sclerenchymatous fibres in *Melampyrum arvense*, *M. cristatum* and *M. nemorosum*, as well as in *Linaria italica*. In *Gratiola officinalis*, L., *Rhinanthus glaber*, Lam., *Melampyrum arvense*, L., *Lindernia pyxidaria*, All., and many species of *Pedicularis* (e.g. *P. palustris*, L.), the **primary cortical tissue** is lacunar[1]. The innermost cell-layer of the primary cortex is in many cases formed by an endodermis, the cells of which either show Caspary's dots on the radial walls, or have their radial walls or all their walls suberized. In other cases an endodermis is not present. The presence of an endodermis is not always characteristic of the genus, although it has been observed for example in twenty-five species of *Veronica* and all investigated species of *Scrophularia* and *Linaria*; thus it is wanting in *Pentstemon gentianoides*, Don and *P. pubescens*, Sol., but is present in *P. procerus*, Dougl. Similarly the differentiation shown by the endodermis is not a generic character; within the genus *Scrophularia* all modifications of this layer are found. The outer limit of the bast shows varied differentiation, but in no case has a typical composite and continuous sclerenchymatous ring been observed. In this region of the stem in *Collinsia bicolor*, Benth., *Mimulus luteus*, L., *Herpestis cuneifolia*, Pursh, *Euphrasia*, *Pedicularis* pro parte and *Rhinanthus* bast-fibres are absent, or only very few isolated fibres occur. In *Linaria grandiflora*, Desf. and *Chelone glabra*, L., there are numerous bast-fibres arranged in bands. Isolated bundles of bast-fibres are stated to occur at the outer limit of the bast in *Pentstemon barbatus*, Nutt., *P. pubescens*, Sol., *P. procerus*, Dougl., *Gratiola officinalis*, L., *Halleria lucida*, L., and *Leucophyllum ambiguum*, Humb. et Bonpl. In *Paulownia* stone-cells occur in the tangential direction between the groups of primary bast-fibres (Möller), but do not lead to the formation of a closed

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[1] It may be noted that in Rhizoma Gratiolae certain groups of the cells, bordering the lacunae, are provided with peculiar ridge-like thickenings on their longitudinal and transverse walls; these thickenings correspond in neighbouring cells (see Vogl, Pharmakognosie, Vienna, 1892, p. 598, Fig. 179).

strengthening ring. In certain other members of the Order the primary bast-fibres unite to form a loose (in *Gerardia flava*, L. and *G. rigida*, Gill.) or a dense cylinder of bast without interspaces (in *Celsia lanata*, Spreng., all investigated species of *Digitalis*, *Paederota Ageria*, L. and *Bartsia alpina*, L.). In this case the ring of hard bast is also connected with the xylem-ring by bridges of fibre-like cells, so that in a transverse section of the stem the groups of soft bast appear like islands embedded in mechanical tissue. As regards the systematic value of these different degrees of differentiation of the hard bast, it is of importance that Born observed all types within the genus *Veronica*; it is therefore evident that the anatomical features in question, at least in some cases, are only of value in specific diagnosis.

The **xylem** invariably forms a dense, closed cylinder; as a rule the vessels are scattered over the whole transverse section, and the individual vascular bundles are not recognizable; in other cases (e.g. in *Antirrhinum Orontium*, L., and *A. majus*, L., *Vandellia crustacea*, Benth. and *Mazus rugosus*, Lour.) the individual vascular bundles are distinct and are separated from one another by radial strips of prosenchymatous cells without vessels. It is a very noteworthy fact that typical medullary rays, i.e. such as are composed of parenchymatous cells, rarely occur in this Order. In my 'Holzstruktur' I laid stress on the absence of medullary ray-parenchyma in *Alonsoa linearis*, Ruiz et Pav., *Calceolaria integrifolia*, L. f., *Castilleja canescens*, Benth. and *Veronica salicifolia*, Forst. f. (all of these being woody plants). Born states that the occurrence or absence of medullary ray-parenchyma is characteristic of the genus, and that typical medullary rays are wanting in all investigated species of *Veronica* and in the Antirrhineae [1] and Euphrasieae, whilst they are present in those Leucophylleae and Aptosimeae which have been examined. In the present Order I have found the medullary rays to be 1–4 cells in breadth; the cells are elongated chiefly in the vertical direction, according to Born. Regarding the detailed structure of the remaining elements of the xylem, attention may be drawn to the following points, the information being derived from my own investigation of species belonging to the genera *Alonsoa*, *Aptosimum*, *Calceolaria*, *Castilleja*, *Esterhazya*, *Freylinia*, *Halleria*, *Leucophyllum*, *Lyperia*, *Manulea*, *Physocalyx* and *Veronica*, as well as from Born's statements. In all cases the vessels do not possess large lumina (maximum diameter =·015 to ·048 mm.). The nature of the bordered pits on the vessel-wall remains unaltered where the vessel is in contact with parenchyma of the medullary rays. Spiral thickening of the vessel-wall is not rare; I have met with it in *Aptosimum depressum*, Burch., *Castilleja canescens*, Benth., *Freylinia undulata*, Benth., *Leucophyllum ambiguum*, Humb. et Bonpl., *Lyperia crocea*, Eckl. and *Veronica salicifolia*, Forst. f.; and Born also found it in *Veronica speciosa*, Cunn., *V. macrocarpa*, Vahl, and *Gerardia rigida*. The perforations of the vessels are invariably simple. The wood-parenchyma is scantily developed. The wood-prosenchyma appears to have simple pits, as stated by Born. In *Freylinia undulata*, Benth., prosenchyma with large, distinct bordered pits occurs side by side with that bearing simple pits (Born). Septation of the wood-prosenchyma has only been observed in *Halleria lucida*, L.

The **pith** is frequently unlignified in the herbaceous species. In *Paulownia imperialis* the young shoots show septation of the pith, which subsequently becomes fistular.

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[1] Herbst's statements (loc. cit.) are not quite in agreement with this.

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OROBANCHACEAE [1].

Both the anatomical structure and the exomorphic features testify to a close relationship with the Scrophularineae and Gesneraceae. The Orobanchaceae, like these two allied Orders, have glandular hairs in which the head is divided by vertical walls only, and stomata which are not accompanied by any special subsidiary cells. Owing to the parasitic habit stomata only appear in reduced numbers. Chlorophyll is not developed in the Orobanchaceae, or is only present in small amount [2]; oxalate of lime is wanting.

The anatomy has been investigated chiefly by Chatin in the genera *Orobanche*, *Phelipaea* (incl. *Anoplanthus*), *Epiphegus*, *Conopholis*, *Boschniakia* and *Aeginetia*, and by Worsdell in *Christisonia*.

The following facts may be pointed out regarding the structure of the **stem**. In most cases there is a single ring of vascular bundles, sometimes possessing secondary growth in thickness. On the other hand **anomalous structure** is found in the following cases: (1) well-developed stems of the more robust species of *Orobanche* (*O. elatior*, Sutt., *O. rubens*, Wallr., *O. caryophyl-*

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[1] The genus *Lathraea*, which is enumerated amongst the Orobanchaceae in Durand's Index, has been described under the Scrophularineae, to which it doubtless belongs.

[2] Cf. Wiesner, in Pringsheim Jahrb., Bd. viii, 1872, p. 582 et seq.

lacea, Sm. and *O. Rapum Genistae*, Thuill.), and the huge stems of *Cistanche lutea*, Link et Hoffmgg., these containing medullary vascular bundles, which enter the vascular ring at a higher level (Solms-Laubach); (2) the axis of *Christisonia neilgherrica*, Gardn., with collateral and concentric vascular bundles (the latter having central phloem) arranged in an irregular ring, and the axis of *C. subacaulis*, Gardn., with scattered bundles, for the most part concentric (with central xylem) in structure (Worsdell); (3) finally, the axis of *Conopholis* and *Epiphegus* with three regular rings of bundles, the individual bundles of which do not unite to form a vascular ring, even in the uppermost portions of the stem. It may be added that in *Epiphegus* the corresponding bundles of the three rings abut on one another in a radial direction, whilst in *Conopholis* they are separated by layers of parenchyma. The differences shown by the stem-structure of those species which have a single ring of vascular bundles is summarized as concisely as is possible by quoting the following series of examples from Chatin's work: *Aeginetia indica*, Roxb. has isolated vascular bundles without hard bast or wood-fibres; *Epiphegus virginianus*, Bart. has isolated vascular bundles provided with hard bast, but without wood-fibres; *Phelipaea indica*, Don and *P. arenaria*, Walp. possess isolated bundles, which are embedded in a closed ring of mechanical tissue composed of fibrous cells; *Phelipaea ramosa*, C. A. Mey. has its vascular bundles united to form a ring, without wood-fibres, but with a ring of hard bast; *Anoplanthus Biebersteinii*, Reut. and numerous species of *Orobanche* have a closed ring of bundles, including wood-fibres, but without hard bast. True medullary rays are not present in the xylem-portions of the vascular bundles, and the vessels, as far as is known, have simple perforations only. The ground tissue of the stem consists of relatively large cells and is mostly divided into pith and cortex by the fibrovascular system. The cortex is lacunar in *Boschniakia glabra*, C. A. Mey.

The **leaves** of the Orobanchaceae investigated by Chatin possess a rather dense and homogeneous mesophyll composed of spherical cells. The leaf-structure in *Epiphegus virginianus* is specially noteworthy owing to the occurrence of numerous pitted cells in the mesophyll; while in *Conopholis americana*, Wallr., the cells of the upper and lower epidermis and those of the lower half of the mesophyll are strongly thickened and pitted.

Stomata are developed on the stem and leaf in most members of the Order (*Orobanche*, *Phelipaea* pro parte, *Anoplanthus*, *Epiphegus*, *Boschniakia* and *Aeginetia*, according to Chatin, and *Christisonia* pro parte according to Worsdell); on the other hand they are wanting in *Phelipaea ramosa* and *Conopholis americana*, according to Chatin, and in *Christisonia bicolor*, Gardn. and *C. subacaulis*, according to Worsdell. Worsdell met with curious anomalous stomata on the stem of *C. neilgherrica*.

The **trichomes** consist of clothing and glandular hairs. The clothing hairs are either quite short and papillose (leaf of *Conopholis americana*), or longer and unicellular (stem of *Phelipaea ramosa*), or short and composed of one or two cells (leaf of *Boschniakia glabra*). Glandular hairs are mentioned by Chatin as occurring in almost all the genera investigated by him (exceptions: *Conopholis* and *Aeginetia*). In these hairs the stalk varies in length and is sometimes very short; it is formed by a single cell, or a row of two or more (never many) cells, the uppermost of which sometimes constitutes a short neck-cell; the head is unicellular, or, owing to the presence of vertical walls, bi- or multi-cellular. The species of *Orobanche*, *Phelipaea*, *Anoplanthus*, *Epiphegus*, and *Boschniakia*, examined by Chatin, have glands with a stalk of varying length and a head composed of two or more cells; the leaves of *Epiphegus virginianus* bear glands with a very short unicellular stalk and a unicellular, bottle-shaped head, whilst the stem has external glands with

longer stalks; ***Christisonia*** has peltate glands with a stalk composed of 1–3 cells and a head of about eight cells.

Literature: Chatin, Anat. comp. d. végét., Pl. paras., 1856 et seq., pl. vii to xxv and pp. 42–130. —Solms-Laubach, in Pringsheim Jahrb., Bd. vi, 1867 and 1868, p. 552 et seq.—L. Koch, Entwicklungsgesch. d. O., Heidelberg, 1887, 389 pp. and 12 Tab.—Hovelacque, Appareil végét. des Bignoniacées etc., 1888, pp. 553 to 634.—Hovelacque, Car. anat. génér. des org. végét. des O. etc., Bull. Soc. d'études scient. de Paris 1889, 11 pp.—Beck, in Natürl. Pflanzenfam., iv. Teil, Abt. 3 b, 1893, pp. 125–6.—Worsdell, *Christisonia*, Ann. of Bot., vol. ix, 1895, pp. 97–136 and pl. v–vi.

LENTIBULARIEAE.

It is well known that the five genera constituting this Order, viz. *Utricularia, Polypompholyx, Genlisea, Pinguicula,* and *Biovularia,* belong to the insect-catching plants. The variety of differentiation shown by the vegetative organs in the individual genera renders it necessary to consider the anatomy separately in each genus. But in the first place it may be noted that, as Goebel points out, the glandular hairs of all the Lentibularieae exhibit a uniform type of structure; they are invariably composed of three parts, viz. a basal cell, one or more stalk-cells, and a head of varied structure; the head is either unicellular or multicellular, and, in the latter case, is divided by vertical walls only. Other features of general interest are as follows: the Caryophylleous type is found in the stomatal apparatus of *Pinguicula* (but not in *Utricularia*); the vascular bundles of the stem in *Utricularia* and *Genlisea* possess the peculiarity that they exhibit a remarkable dissociation and mutual independence of the xylem and phloem. Oxalate of lime has rarely been observed [1] (leaf of *Utricularia montana*); when present it occurs in the form of small, spindle-shaped crystals.

1. *Pinguicula.*

The species of *Pinguicula,* as is well known, are plants possessing numerous true roots and a considerable number of simple leaves, united into a radical rosette; the leaves are covered with sticky glandular hairs, and have the power of infolding their margins when stimulated.

The structure of the **axis**, which has been examined in *P. alpina* and *P. vulgaris* by J. Klein and Hovelacque, shows no special features; there is an ordinary ring of bundles; an endodermis is scarcely recognizable. Contrary to Hovelacque's statements, Dangeard describes polystely in the subterranean axis of *P. vulgaris* (this is incorrect according to Hovelacque), and in a few other species (*P. lutea, P. lusitanica* and *P. longifolia*). The vascular system in these species, as in *Primula Auricula,* is said to consist of several annular strands in the transverse section; each of these has a central pith surrounded by a ring of xylem- and phloem-groups; external to these lies a 'réseau radicifère,' differentiated in an annular manner; then a pericycle of one or two layers follows, the whole being surrounded by an endodermis.

The following facts may be mentioned regarding the **leaf-structure** of *P. vulgaris* and *P. alpina.* The mesophyll consists of more or less isodiametric cells. The epidermal cells of the leaf contain no chlorophyll. In *P. alpina* one or more crystalloids have been shown to occur in the nuclei of the epidermal cells. Stomata are stated to occur only on the lower surface of the leaf in *P. vulgaris,* on both sides in *P. alpina.* In both these species the pair of guard-cells is as a rule accompanied by two or more subsidiary cells, placed transversely to the pore, but exceptions to this type occur. In *P. alpina* the stomata are sometimes to be found in pairs. With regard to the **glands** (Fig. 136), the structure of those of *P. alpina* may first be described by quoting from J. Klein's statements. The glands are of two kinds, some being stalked and occurring on the upper side of the leaf, while others are sessile, and are found on both surfaces. The stalked glandular hairs consist of a basal cell, which is an epidermal cell arched outwards, and a stalk-portion formed by 1–4 cells. At the apex of the stalk there is a small cell, which extends upwards

[1] According to J. Klein and Zimmermann nuclear crystalloids occur in the genera *Pinguicula* and *Utricularia.*

into the body of the gland, like the columella in a sporangium of *Mucor*; it may therefore be called a columella. The body of the gland is seated upon it like a cap, which appears disc-shaped in surface-view, and consists of a layer of cells arranged in a radiate manner, but the vertical walls do not all extend to the centre of the disc. The glandular head first becomes divided into quadrants by means of two vertical walls bisecting one another at right angles; the quadrants then undergo further division by secondary vertical walls placed obliquely to those first formed. In *P. alpina* the basal and stalk-cells contain nuclei with crystalloids; these bodies are also present in the nuclei of the cells forming the glandular disc, when these cells are at relatively early stages of development. The glands borne by the middle portion of the leaf have long stalks, but towards the margin of the leaf the stalk is unicellular. The sessile glands have essentially the same structure as those with stalks, except for the absence of the stalk. They are more or less depressed, and consist of a basal cell, a stalk-cell (=columella), and the gland, only a portion of which generally projects above the epidermis. The body of the gland consists of 2–10 cells, or even more. It may be noted that the glands composed of few (2–4) cells lie at the margin of the leaf, whilst those with more numerous cells are to be found near the midrib. In the case also of glands composed of numerous cells, four quadrant cells are formed in the first place by two vertical walls intersecting one another at right angles. In *P. vulgaris* simple uniseriate hairs with thin walls occur intermingled with glands having a structure similar to that above described. According to Haberlandt the shortly stalked glands on the upper side of the leaf of *P. vulgaris* have a digestive function, and the same probably applies to the long-stalked glands on the same surface; the latter excrete the mucilage necessary for the retention of the insect. The shortly stalked glands on the lower side of the leaf excrete and also absorb water.

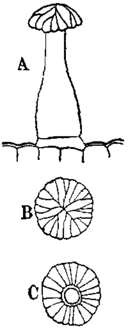

FIG. 136. External glands of *Pinguicula alpina*, L.; in B and C the gland is separated from the stalk, and is seen from above in B, from below in C.—After J. Klein.

2. *Genlisea.*

Genlisea, the second genus of the Lentibularieae, comprises plants which are destitute of roots, and possess radical rosettes of numerous simple leaves, and, in addition, have other leaves inserted on the rhizome and transformed into tubular ascidia of complicated structure. The largest species, *G. ornata*, Mart., is that in which the anatomy is best known through the researches of Warming, Darwin and Goebel; Darwin also makes a few statements on the anatomy of *G. africana*, *G. aurea* and *G. filiformis*.

The fibrovascular system of the **stem** of *G. ornata* is very peculiar, recalling that of certain Utricularias, especially *Utricularia montana*, Jacq. Actual vascular bundles, composed of phloem and xylem, are not present. The phloem-strands constitute a network, owing to anastomosis, and form an independent system separated by parenchyma from the annular xylem, which encloses a pith. To provide the vascular supply of the leaf, a phloem- and xylem-strand pass out from this fibrovascular system; the two unite and form the leaf-trace. It may be added that the peduncle possesses a similar structure, though it contains a mechanical cylinder of strongly lignified cells, sometimes enclosing strands of phloem, while the xylem- and phloem-systems are less sharply separated than in the stem.

According to Goebel, the ordinary **foliage leaves** of *G. ornata* are covered with a layer of mucilage, which is excreted by numerous glandular hairs. These hairs consist of a basal cell sunk in the epidermis of the leaf, a short stalk-cell, and a spherical terminal cell, which produces the secretion. Stomata are entirely absent.

Finally, the anatomy of the **ascidiform leaves**, which has been described by Goebel, remains to be discussed. First, however, the shape and the component parts of these leaves may be briefly referred to. The ascidium (Fig. 137 *A*) consists of three parts: (1) a basal portion; (2) the actual tube, which is composed of a bladder-like enlargement (bladder) adjoining the basal portion, and a long neck-like part (neck); (3) the two spirally twisted arms, which are situated at the end of the tube. The tube has a slit-like opening between the two arms, or, to express it more correctly, a row of small separate apertures. The two arms originate on

either side of this slit in the form of protuberances, which continue their growth by means of special apical meristems; in this way both the cavity of the tube and also the slit become elongated in the direction of the arms. The two apices, in their further growth, revolve round their own axes, so that the arms appear spirally twisted, and provided with a similarly twisted slit; this, as in the case of the slit between the arms, consists of a large number of separate apertures. In the anatomy of the tubular leaf the following points are noteworthy. The basal portion is traversed by a rather weakly developed vascular bundle. At the base of the enlarged cauldron-like portion (the bladder) this bundle divides into two

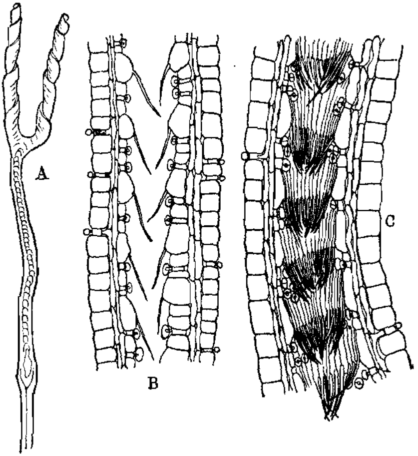

FIG. 137. *Genlisea ornata*, Mart. A, General appearance of a tubular leaf; B, Longitudinal section from the neck-portion; C, Longitudinal section through one arm.—After Goebel.

branches, of which one extends upwards on the dorsal, the other on the ventral side of the tube; at the upper end of the tube each of these branches divides again into two, so that a pair of vascular bundles is given off to each arm. The structure of the internal portion of the tube in the region of the neck (Fig. 137 *B*) is very interesting; it resembles an eel-trap. A large number of long, simple, pointed hairs project into the interior, the ends of these hairs being directed towards the base of the tube. These hairs have a zoned arrangement, since they spring from cells of the inner epidermis forming annular zones, each of which is only one cell in breadth; these epidermal cells are slightly arched outwards like papillae, and have an elongated, four-sided outline; the hairs themselves consist of two cells, a transverse wall being formed near the tip. Taken together these hairs form funnels, the narrow openings being directed towards the basal portion of the tube. Large numbers of these funnels are found in the region of the neck; they appear to be inserted one within the other, since the annular zones of four-sided epidermal cells, which form the margin of the wide upper opening of the funnel, are only separated from one another by a few rows of cells. The bands of cells separating the annular zones of four-sided elements from one another consist of smaller epidermal cells; these have an undulated outline, and between them numerous short glandular hairs excreting mucilage arise; these hairs consist of a basal cell, a short stalk-

cell, and a bicellular head with a vertical division-wall; stomata also occur in this zone. In the lower portion of the neck the funnels are wanting; here, however, as in the bladder, glands occur, bearing a bicellular head, but lower down, they are replaced by glands with a head of 4–8 cells. These are developed in large numbers in the lower portion of the tube, especially along two longitudinal lines, corresponding to the position of the vascular bundles. The arms (Fig. 137 *C*) show the same kind of eel-trap hairs as the tube; they are not, however, arranged in annular, but in transverse zones, and together they form a spiral line. Regarding the origin of the separate apertures on the arms and between them, see Goebel, loc. cit.

In addition to *G. ornata*, the two species *G. africana* and *G. aurea* have been examined, and were found to show the same features. On the other hand, according to Darwin, *G. filiformis* differs in the absence of ascidiform leaves of the type otherwise characteristic of the genus, but bladders occur, like those of *Utricularia*, and the internal epidermis bears glandular hairs with four arms, as in *Utricularia*, the arms being of equal length.

3. *Utricularia.*

This genus, as is well known, resembles *Genlisea* in having no roots. Some of the species of *Utricularia* are land-plants and some are water-plants; their external conformation shows a type of differentiation which is often rather extreme and also very remarkable; details are to be found especially in Goebel's works. From his investigations Goebel comes to the conclusion that the distinction between axis and leaf must be abandoned in the Utricularias; for one meets with leaves, which are capable of growing out into organs possessing almost all the characters of a shoot, while on the other hand long cylindrical stolons, bearing bladders, sometimes (e.g. in *U. rosea*) become flattened at the tip, and converted into a leaf.

In the following paragraphs we will deal with the anatomical structure of the axis, of the leaves and of the peculiar bladders, which are modified as traps for animals.

According to H. Schenck, a transverse section of the **axis** of the inflorescence of *Utricularia montana*, Jacq. (Fig. 138 *A*) shows a peculiar type of structure, which is also found in *U. Schimperi*, H. Schenck, and other species (see Merz, loc. cit.), although it is not always equally well marked; it recalls the features described above in *Genlisea ornata*. The wood- and bast-portions of the vascular bundles appear separate and independent of one another. The transverse section shows a pith, with scattered strands of soft bast and surrounded by an annular zone containing the xylem-groups; outside this zone we find a ring of mechanical tissue, which is composed of fibrous cells with walls of varied thickness, and contains scattered bundles of soft bast; this is followed externally by the endodermis and the cortical tissue. The thicker portions of the rhizome have a structure similar to that of the axis of the inflorescence. According to H. Schenck, the structure of the axis in *U. vulgaris* and *U. minor* (Fig. 138 *B*) is somewhat different, although it may be referred to the type found in *U. montana*. In the central strand the endodermis is adjoined by an annular zone of phloem-groups, which are separated from one another by parenchymatous cells having wider lumina and passing over internally into a 'pith' composed of somewhat collenchymatous cells (homologous with the mechanical tissue of *U. montana*); in correspondence with the submerged mode of life only a few vessels are developed, and they are situated towards the lower side of the small floating stem, so that dorsiventral structure is attained. An endodermis can be demonstrated in almost all the species of *Utricularia* (Kamienski). Mechanical tissue, as shown by the examples quoted above, is not always present, but it is particularly strongly developed in *U. neottioides*, St. Hil. Large air-spaces, often exhibiting a regular arrangement, may be observed in the well-developed cortex and sometimes also in the pith of the aquatic Utricularias.

The anatomy of the very variously shaped **foliage-leaves** of the Utricularias has hitherto been little examined. According to Schimper the subterranean cylindrical portions of the leaves of *U. cornuta* consist of lacunar, elongated parenchyma, which surrounds an axile vascular bundle, and is clothed by an epidermis of elongated cells; the epidermis contains numerous small capitate glands, possessing a cylindrical basal cell, a cell forming the stalk, and another forming the head. The green portions of the leaves consist of short cells; here the glandular hairs

are less numerous, and stomata are present near the margin of the leaf. According to Hovelacque, the aerial leaves of *U. montana*, when seen in transverse section, exhibit a mesophyll showing little differentiation, although provided with larger intercellular spaces on the lower side of the leaf. In this species the cells of the upper epidermis contain small spindle-shaped crystals of oxalate of lime; on the lower surface stomata are present, which are not accompanied by any special subsidiary cells. The hairy covering on the leaf of *U. montana* is likewise composed of short capitate hairs with a unicellular head. Finally, to give a third example, the aquatic leaves of *U. vulgaris* show, in transverse section, a homogeneous mesophyll enclosed by the epidermis; the mesophyll is composed of isodiametric cells, and contains intercellular spaces, and an axile fibrovascular strand exhibiting the same structure as that in the stem. The epidermis of the leaf, like that of the stem, bears capitate hairs with a cylindrical basal cell inserted between the epidermal cells, a short stalk-cell and a head, divided into two cells by a vertical wall.

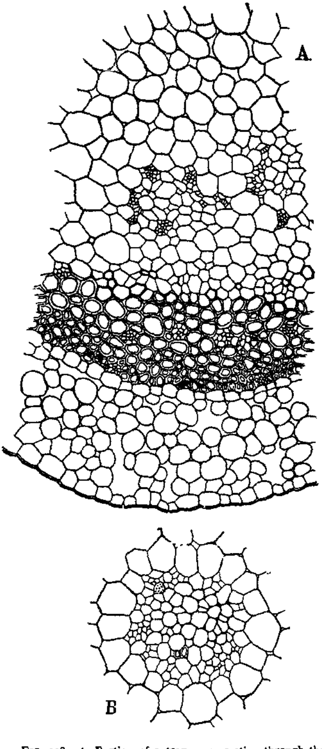

FIG. 138. A, Portion of a transverse section through the axis of the inflorescence in *Utricularia montana*, Jacq.; B, Transverse section through the axile strand in the axis of *U minor*, L.—After H. Schenck.

The **bladders** or ascidia of *Utricularia*, as is well known, are more or less distinctly stalked, spherical or ovoid, bladder-like structures, which are somewhat compressed laterally, hollow, and provided with a lateral aperture (Fig. 139 *A*). The part of the bladder limiting the aperture on the upper side, is best described as the upper lip, and the portion bounding it below as the lower lip. The upper lip becomes broader towards the interior of the bladder and forms an elastic lid or trap-door, like a curtain, which, although permitting the entry of small animals into the bladder, prevents their exit. It may also be noted that the upper lip of the bladder is very commonly produced into trichomes or emergences; the latter bear hairs of different kinds, vary in shape, and are termed antennae, owing to their resemblance to the extremities of certain Crustacea (Daphnideae). The anatomical structure of the bladders has been examined especially in *U. vulgaris* (by Cohn, Hovelacque and others), in *U. neglecta* (by Darwin), in *U. cornuta* (by Schimper) and in *U. flexuosa* (by Goebel). The wall of the mature bladder (Fig. 139 *A*), excluding the lower lip, consists of two layers of cells; a third middle layer, originally present, has disappeared in the fully-developed bladder. In a longitudinal section through the bladder, the lower lip

is seen to consist of a massive tissue of several layers of cells. The lid shows the same structure as the wall of the bladder, i.e. it is composed of two layers of cells; it may be noted that the cells of the outer layer of the lid are concentrically arranged around an organic centre (*U. vulgaris* and *U. flexuosa*). The bladder is traversed by two vascular bundles, the course of the one being median on the dorsal side, that of the other median on the ventral side of the bladder. In the different species these vascular bundles extend to a varying distance towards the aperture. In *U. flexuosa*, for example, the dorsal bundle disappears a short distance before reaching the front of the bladder, whilst the ventral branch extends as far as the point at which the

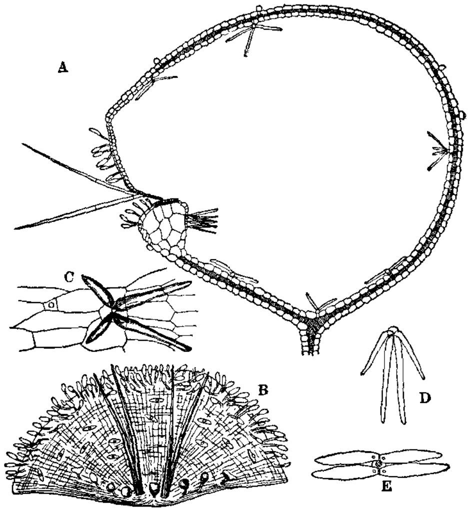

FIG. 139. A, Longitudinal section through a bladder of *Utricularia flexuosa*; B, The lid of the bladder of *U. neglecta*; C–E, Four-armed glands on the inner wall of the bladder; C, *U. neglecta*; D, *U. minor*; E, *U. montana*.—A after Goebel, B–E after Darwin.

lower wall of the bladder becomes thickened to form the lower lip. The outer wall of the bladder (omitting for the present the upper and lower lips, which will be considered separately) is provided with short external glands, consisting of a basal cell, a stalk-cell, and a head; the latter may be unicellular and spherical (*U. cornuta*) or bicellular and bilobed, like an anther of the Euphorbiaceae (*U. vulgaris*). The variously shaped antennae commonly bear ordinary uniseriate hairs, sometimes also mucilage-hairs, e.g. in *U. coerulea* and *U. elachista*, according to Goebel; in the former species these mucilage-hairs consist of a basal cell, a short stalk-cell, and a long sac-like terminal cell, whilst in *U. elachista* the stalk-cell and the terminal cell are equally elongated. The lid[1] and the lower lip bear a peculiar type of hairy covering, which is certainly connected with the function of the bladders. In *U. neglecta*, for example (Fig. 139 *B*), the species investigated by Darwin, two pairs of bristles are found on the middle of the lid, though rather

[1] The lid of the bladders in *U. montana*, however, bears no hairs (Hovelacque).

nearer to its free internal margin; they are formed by simple uniseriate hairs. Between them we find glands with a short stalk and a rather large, spherical, bicellular head, and similar glands occur on either side of the bristles, all the glands together forming an arc, parallel to the free margin of the lid. The front margin of the lid is covered by numerous glands composed of three cells, viz. a rather long stalk-cell, a shorter neck-cell, and an ellipsoidal terminal cell; on the middle portion of the surface of the lid there are shortly stalked glands, the bicellular terminal portion of which is two-armed. Goebel describes the same types of glands exhibiting the same arrangement (except in the case of the two-armed hairs) on the lid of the bladder in *U. flexuosa*, and the lid in *U. vulgaris* shows a similar structure. The hairs on the lid, all those in fact in the neighbourhood of the aperture, are regarded as baits for the attraction of aquatic insects. The glandular nature of the lower lip (Fig. 139, *A*) probably serves the same purpose. On the outer portion of the lower lip (in *U. vulgaris* and *U. flexuosa*, for example), stalked, three-celled, glandular hairs are found of the same type as those on the outer margin of the lid, viz. hairs with a rather long stalk-cell, a shorter neck-cell and an ellipsoidal terminal cell. The epidermis of that part of the inner side of the lower lip which borders on the aperture, is entirely transformed into a tessellated epithelium in the two species mentioned, and also in *U. cornuta*; for it is replaced by a group of crowded glands, each composed of three cells. Finally, in *U. flexuosa* and *U. vulgaris*, the internal wall of the lower lip, facing the interior of the bladder, bears two-armed hairs with upwardly directed arms; they consist of a basal cell, a short stalk-cell and two terminal cells, which are directed upwards like arms. These two-armed hairs do not appear to occur on the lower lip in all species of *Utricularia*; Schimper figures simple, stalked, glandular hairs in place of them in *U. cornuta*. Other glands of a peculiar type (Fig. 139, *C–E*) are found on the inner wall of the bladders of *Utricularia*. These glands possess a two- or four-armed terminal portion, composed of two or four cells besides the stalk-cell and basal cell; they are regarded as organs for the absorption of the decaying bodies of animals. The two or four arms of these glands lie in one plane, parallel to the wall of the bladder. Two-armed glands are said to occur on the inner wall of the bladders in *U. coerulea*, *U. cornuta*, and *U. Griffithii*, four-armed hairs in *U. amethystina*, *U. minor*, *U. montana*, *U. multicaulis*, *U. neglecta*, *U. nelumbifolia*, *U. orbiculata* and *U. vulgaris*. According to Darwin the four-armed glands differ in the relative position and in the length of their arms in the individual species. In *U. vulgaris* and *U. neglecta* (Fig. 139, *C*), the arms, which together form an *X*, are arranged in pairs of unequal length, the longer pair of arms being directed towards the posterior end of the bladder (i.e. the end remote from the aperture). In *U. minor* also (Fig. 139, *D*), two of the arms are longer than the other two, but here both pairs are turned in the same direction. The four-armed glands of *U. orbiculata* and *U. multicaulis* have arms of equal length. Finally, in *U. montana* (Fig. 139, *E*) the four arms, which are arranged in pairs of unequal length, have been shown to have a peculiar orientation; the two longer arms lie in an approximately straight line, the two shorter arms in a second straight line, parallel to the first.

4. *Polypompholyx*.

The species of this small genus possess typical *Utricularia*-bladders, which have been investigated in a general comparative manner by Darwin in *P. multifida* and *P. tenella*. On the bladders the pairs of antennae, so widely distributed in the species of *Utricularia*, are replaced by a small membranous fork, the basal portion of which forms a kind of cap over the entrance to the bladder. The inner surface of this cap is covered with long, simple hairs, which according to Darwin probably have an absorptive function. Besides these one finds on the lower lip 'numerous one-celled papillae, having very short foot-stalks.' The inner wall of the bladders is provided with four-armed glands, in which the diverging arms are of equal length. It may be added that in *P. laciniata*, Benjamin (in the Flora Brasiliensis, vol. x, 1847, Tab. xxii, ii) figures glands with a uniseriate stalk and a disc-shaped head, showing the same structure as the glands of *Pinguicula*; these glands also occur on the sepals and bracts.

5. *Biovularia*.

A detailed investigation of this monotypic genus, which also possesses bladders, has not yet been made. Kamienski, in the Natürliche Pflanzenfamilien, merely states that *Biovularia* approximates to the small aquatic species of *Utricularia* in its morphological and anatomical features.

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COLUMELLIACEAE.

In this small Order, which includes only the single genus *Columellia* with a few species, *Columellia serrata*, Rusby (Bang, n. 1172, Bolivia) was examined. The structure of the wood presents a number of very characteristic features, viz.: (*a*) vessels having small lumina (diameter = ·021 mm.), scalariform perforations with numerous bars, and bordered pits on the walls, including those in contact with parenchyma of the medullary rays; (*b*) uniseriate medullary rays; (*c*) scantily developed wood-parenchyma; and (*d*) wood-prosenchyma provided with distinct bordered pits. The cork arises at the outer limit of the bast, and consists of layers of radially elongated cork-cells alternating with layers of cells which have cellulose walls and are compressed in the radial direction. Oxalate of lime is present in the axis in the form of clustered crystals (in the pith and primary cortex), and of solitary crystals, mostly resembling styloids (in the bast of older branches). The structure of the leaf is bifacial, and the stomata, which only occur on the lower side, are surrounded by a relatively large number of ordinary epidermal cells. The hairs, developed on the lower side of the leaf, are simple and unicellular; close to their point of insertion they are bent back against the epidermis, and are adpressed to the leaf; glandular hairs are not present. Finally, the occurrence of a one-layered hypoderm on the upper side of the leaf in *Columellia serrata* remains to be mentioned; the cells of this layer, like those of the epidermis on both sides of the leaf, have polygonal outlines.

The position of the Columelliaceae in the Natural System is still uncertain. On the ground of their exomorphic characters a relation to the Gesneraceae and Saxifragaceae has been suggested. The anatomical features previously referred to, especially the lack of glandular hairs, the occurrence of none but scalariform perforations in the vessels, and of wood-prosenchyma bearing bordered pits throughout, are not quite favourable to a very close affinity with the Gesneraceae, whilst scalariform perforations and prosenchyma with bordered pits are widely distributed in the Saxifragaceae; in that Order glandular leaf-teeth and trichomes similar to those of *Columellia serrata* also occur.

GESNERACEAE.

Relatively little has been done in the anatomical investigation of this Order, but such researches as have been carried out tend to show that the Gesneraceae are not distinguished by any constant anatomical feature from the allied Orders Scrophularineae and Bignoniaceae. As in these two Orders, the vascular bundles are simply collateral, oxalate of lime is chiefly excreted in the form of small acicular crystals, the heads of the glandular hairs are divided exclusively by vertical walls, the perforations of the vessels are simple, and the wood-prosenchyma bears simple pits. In addition to the acicular crystals clustered crystals have been observed, and, besides the glandular hairs, there are simple uniseriate trichomes (Fig. 140), which sometimes have a very strongly thickened terminal cell. Even on the mature leaf the stomata are mostly surrounded by three epidermal cells, which sometimes have the appearance of subsidiary cells. The development of cork is superficial or internal.

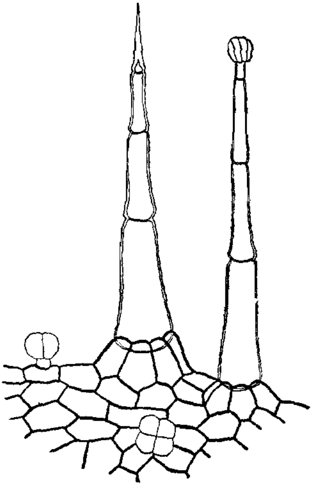

FIG. 140. Hairy covering of *Achimenes grandiflora*, DC. —Original.

Our knowledge of the **leaf-structure** of the Gesneraceae[1] is based on Vesque's general comparative investigations, which extended to species of the genera: *Aeschynanthus*, *Chirita*, *Columnea*, *Episcia*, *Gesnera*, *Moussonia*, *Nematanthus*, *Ramondia*, *Rhytidophyllum*, *Sciadocalyx*, and *Tydaea*; while Hielscher has examined the leaf of *Streptocarpus*, which, as is well known, must be regarded as being morphologically a cotyledon. In all these species the leaf-structure is bifacial, and this also applies to *Streptocarpus polyanthus*, Hook. The spongy tissue in this plant shows a peculiar structure; it consists of spherical cells, which exhibit annular thickenings on those parts of their walls which adjoin intercellular spaces. In certain cases (*Episcia*, *Tydaea gigantea*, *Moussonia elegans*, *Gesnera longifolia*) the **epidermal cells** on the upper side of the leaf are strongly developed, and serve as water-receptacles; sometimes (*Gesnera zebrina*) this differentiation extends to both upper and lower epidermis. Other species are distinguished by a **hypoderm**, which serves for the storage of water, and sometimes (*Aeschynanthus grandiflorus*) consists of many layers, in this case occupying almost one-third of the thickness of the leaf. According to Vesque, the following species have a hypoderm: *Chirita sinensis*, *Aeschynanthus pulchra*, *A. grandiflora*, *Nematanthus Guille-*

[1] The scale-leaves, which occur on the runners in many members of the Order, have not, as far as I am aware, been examined anatomically; they may therefore be recommended as a subject fo investigation.

minianus, and *Columnea Schiedeana*. The **stomata**, as stated above, belong to the Cruciferous type, and this is usually recognizable even in the mature leaf. The three epidermal cells, surrounding the guard-cells, are differentiated as subsidiary cells (being much smaller than the remaining cells of the epidermis); this is the case, according to Vesque, in the species just quoted as possessing a hypoderm, and also, according to Benecke, in a plant, described as '*Agalmyla inaequafolia*'; in *Tydaea gigantea*, *Moussonia elegans*, *Gesnera zebrina*, *G. longifolia*, and *Rhytidophyllum crenulatum*, on the other hand, the cells adjoining the guard-cells are not specially prominent, according to Vesque, and these plants also possess no hypoderm. The stomata either lie on a level with the epidermis, or (*Rhytidophyllum crenulatum* and *Episcia Luciani*) project considerably. Cork-warts have been observed on the leaves of *Aeschynanthus pulchra* and *A. splendens* (E. Bachmann).

Oxalate of lime usually appears in the axis and leaf in the form of crystals resembling the envelope of a letter, small prisms and acicular crystals; those of the last type are sometimes (*Gesnera zebrina*) rather long, and resemble raphides. In *Cyrtandra biflora*, Forst., I observed small clustered crystals in the pith and primary cortex; they are composed of loosely connected acicular and spiniform crystals [1].

The **trichomes** (Fig. 140) are (1) simple, uniseriate clothing hairs, and (2) glandular hairs. The clothing hairs usually consist of a relatively small number of cells, and mostly have smooth walls. Their characteristic feature lies in the fact that the terminal cells are (at least at the apex) more strongly thickened than the remaining cells of the hair, which have wide lumina and rather thick walls; sometimes (species of *Achimenes*, *Gesnera*, *Isoloma*, *Rhytidophyllum*, according to A. Weiss and Vesque) the terminal cell is so much thickened as to cause obliteration of the lumen. When this is the case, the hairy covering appears very rough. It may be added that the cells of the hair frequently have red or blue cell-sap, and consequently contribute materially to the ornamental appearance of the plant, and that the hair not uncommonly springs from the middle of a pedestal composed of two or more cells. The glandular hairs do not differ from those of the Scrophularineae. The stalk is of varied length, and may consist of one or more cells. The head is almost always [2] divided by vertical walls only, into two, four, six, or more cells. In the same species glands with short and long stalks, and having a varied number of cells in their heads, sometimes occur side by side. Glandular hairs have been observed in species of *Aeschynanthus*, *Chirita*, *Columnea*, *Episcia*, *Gesnera*, *Isoloma*, *Moussonia*, *Nematanthus* and *Sciadocalyx*.

The course of the **vascular bundles** and the correlated structure of the **petiole** are of systematic value according to Hollstein and Fritsch. All the species [3] investigated by Hollstein belonging to the Gesnerioideae (of Fritsch's classification), as well as certain other species, have leaf-traces consisting of a single strand. In the petiole two or more small vascular bundles are present, in addition to the principal strand; but as a rule they fuse with it while still in the petiole. On the other hand the members of the Columneae [4] (of Fritsch's system) which have been examined, as well as *Gonatostemon Bouchea-*

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[1] Raunkjär met with nuclear crystalloids in the epidermis of the leaf in species of *Aeschynanthus* and Zimmermann found them in the veins of the leaf in a plant described as *Gloxinia hybrida*.

[2] Only exceptionally ('par accident') do horizontal divisions also occur in the head, e.g. in the long-stalked glands on the corolla of *Columnea erythrophaea* (Vesque).

[3] Namely species of *Gesnera*, *Achimenes*, *Aeschynanthus*, *Codonophora*, *Diastema*, *Dicyrta*, *Eucodonia*, *Gloxinia*, *Guthnickia*, *Houttea* (?), *Isoloma*, *Koellikeria*, *Kohleria*, *Ligeria*, *Locheria*, *Mitraria*, *Niphaea*, *Rechsteineria*, *Rhytidophyllum*, *Rosanovia*, *Scheeria* and *Streptocarpus*.

[4] Species of *Alloplectus*, *Alsobia*, *Besleria*, *Columnea*, *Cyrtodeira*, *Episcia*, *Houttea* (?), *Nematanthus* and *Paradrymonia*.

num, Reg., have three distinct leaf-trace strands. An exceptional position is held by *Klugia Notoniana*, in which a transverse section of the stem exhibits medullary vascular bundles, while the leaf-trace consists of a relatively large number of separate vascular bundles; some of these enter the vascular ring of the axis, others traverse the pith as medullary bundles.

The structure of the **axis** has been examined by me in *Pentarhaphia longiflora*, Lindl., *Bellonia spinosa*, Sw., *Alloplectus cristatus*, Mart., and *Cyrtandra biflora*, Forst. The **wood** possesses medullary rays of varying breadth and vessels of varied diameter (maximum diameter between ·03 and ·108 mm.). The perforations of the vessels are simple throughout. The walls of the vessels, where they are in contact with parenchyma of the medullary rays, usually bear bordered pits only, but in *Alloplectus cristatus* there are simple pits as well. The wood-parenchyma is scantily developed. The pitting of the wood-prosenchyma may be described as simple; the lumina of the elements forming this tissue are commonly septate in the four species mentioned above. In *Rhytidophyllum tomentosum*, Mart., in which Pomrencke examined the structure of the wood, we find the same features as in *Pentarhaphia*, &c. In the structure of the **cortex** it may first be noted that the development of cork may take place superficially, viz. in the epidermis (*Columnea Schiedeana*, according to Douliot), or subepidermally (*Alloplectus*, *Cyrtandra*); or its position may be internal to the sclerenchyma of the pericycle (*Bellonia*, *Pentarhaphia*, as well as *Rhytidophyllum Plumerianum*, according to Douliot). The cork-cells have thin walls in *Pentarhaphia*; the outermost lamellae of their walls are lignified in *Bellonia*, whilst in *Alloplectus* and *Cyrtandra* some of the cork-cells have their inner tangential walls sclerosed. The outer portion of the primary cortex is sometimes (*Pentarhaphia*, *Cyrtandra*) collenchymatons; stone-cells are found in the primary cortex in *Alloplectus cristatus*, whilst cells, with sclerosed walls resembling a horse-shoe in transverse section, occur in *Aeschynanthus grandiflorus* (according to Vesque). In the pericycle, in the species of *Pentarhaphia*, *Bellonia* and *Cyrtandra* referred to above, as well as in *Rhytidophyllum Plumerianum*, according to Douliot, there are groups of more or less elongated, pitted sclerenchymatous cells resembling rod-cells, and having yellow walls; they are wanting in *Alloplectus cristatus*. In *Pentarhaphia longiflora* the sclerenchymatous pericycle is strengthened by a few layers of suberized cells, which are situated externally to it, and are derived from the primary cortical parenchyma. The same species contains rod-cells in the secondary bast.

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BIGNONIACEAE.

1. Review of the Anatomical Features. The frequent occurrence of anomalous types of structure in the axis is specially characteristic of this Order, which includes many lianes. Four different kinds of anomalies have been observed: (I) Wedges of bast in the xylem-mass (Fig. 142, *A–B*); they are present in definite numbers (4, 8, 16, and so on), and are specially distinguished by possessing cambium on their inner side only, and not on their radial surfaces; in transverse section they are bounded towards the adjacent

projecting portions of the wood by a straight line or by a series of steps; (II) Secondary zones of growth arising in the cortex; (III) Ultimate fission of the xylem-mass (Fig. 142, *C*); (IV) Strips of wood and bast occurring at the margin of the pith and showing inverted orientation. Otherwise there are no special characters sharply separating the Bignoniaceae from the allied Orders. The type of stoma varies; the pair of guard-cells is either surrounded by three or more epidermal cells, or there are subsidiary cells placed parallel to the pore. The vessels of the wood have simple perforations; the wood-prosenchyma bears simple pits; the development of cork is mostly superficial, and the phloem shows a tendency towards stratification into hard and soft bast. Accompanying simple, unicellular or uniseriate hairs and multicellular, branched trichomes, glandular hairs of varied structure are found; the latter all agree in so far as the head is divided by vertical walls only; the large patelliform glands, found in certain members of the Order, may be specially pointed out (Fig. 141, *E*). Oxalate of lime is usually excreted in the form of small acicular crystals or small crystals of the ordinary type, but also occurs in the form of clustered and large solitary crystals. The following special features, which may be employed in detailed anatomical diagnosis, have been observed: development of hypoderm in the leaf; sclerenchymatous fibres running freely in the mesophyll; groups of sclerenchymatous fibres in the outer cortex of the branch.

2. STRUCTURE OF THE LEAF. The leaf-structure has only been examined in a general comparative manner by Vesque and Hovelacque. The **mesophyll** usually has bifacial structure. In *Campsis radicans* and *Ducoudraea capensis* a layer of cells with very wide lumina occurs at the limit between palisade and spongy tissue; in *Colea Commersonii* sclerenchymatous fibres running freely in the mesophyll are present. The **epidermal cells** may have straight or undulated lateral walls; the cuticle may be smooth, striated, or (*Colea*) verrucosely thickened. Gelatinization of the epidermis of the leaf has not been observed. The epidermal cells on the upper side of the leaf in species of *Catalpa*, *Crescentia*, and *Colea* are distinguished by their considerable height; *Tecoma leucoxylon* is characterized by the occurrence of horizontal division-walls in the epidermal cells; *Pandorea jasminioides* and *Schlegelia parasitica* are distinguished by the occurrence of a hypoderm, composed of one or several layers respectively, on the upper side of the leaf. The **stomata** in the species investigated are only found on the lower side of the leaf. In most cases (species of *Bignonia*, *Catalpa*, *Stizophyllum* and *Tecoma*, according to Vesque, and of *Amphicome*, *Amphilophium*, *Campsis*, *Clytostoma*, *Cuspidaria*, *Ducoudraea*, *Eccremocarpus*, *Incarvillea*, *Melloa*, *Pandorea* and *Stenolobium*, according to Hovelacque) the pairs of guard-cells are surrounded by a considerable number of ordinary epidermal cells; in *Crescentia Cujete*, however, one finds on the same leaf-surface stomata with three subsidiary cells, and others with two subsidiary cells, parallel to the pore, while in *Adenocalymna marginatum* and other species, *Bignonia triplinervia*, *Colea Commersonii* and *Schlegelia parasitica*, the stomatal apparatus, without exception, follows the Rubiaceous type (i.e. two or more subsidiary cells are placed parallel to the pore on both longitudinal sides of the pair of guard-cells).

The structure of the **petiole** and of the veins of the leaf is so varied, that I can only refer to the statements made by Hovelacque, Petit and Vesque on this subject.

The **hairy covering** consists of clothing and glandular hairs. The clothing hairs are usually simple, unicellular or uniseriate trichomes, with relatively wide lumina and fairly thick walls, the external surface of which may be smooth or covered with irregularities. Both kinds, viz. unicellular and uniseriate clothing hairs, may occur side by side in the same species (e.g. *Bignonia exoleta*).

In addition to the trichomes just mentioned, branched, multicellular clothing hairs have been met with in this Order (by Bureau in *Adenocalymna*, *Amphilophium* and *Pithecoctenium*, by Bureau and Schumann in *Arrabidaea* and *Tecoma*, and lastly in *Zeyheria montana*, Mart.). The branched trichomes of *Amphilophium Mutisii* (according to Hovelacque) and of *Arrabidaea corchoroides*, P. DC., and *A. macrophylla*, K. Sch. (according to Bureau and Schumann) vary in the degree of their branching; they possess a uniseriate main axis and unicellular or uniseriate lateral branches of the first and sometimes

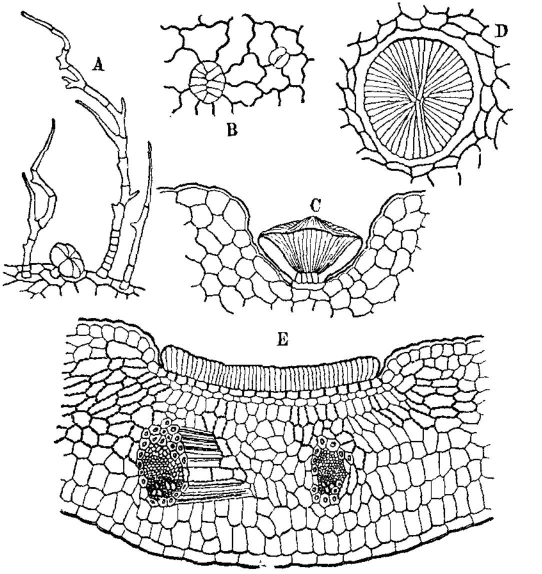

FIG. 141. Hairy covering of the Bignoniaceae: A, *Tecoma mollis*, H.B.K.; B, *Amphicome arguta*, Royle; C–D, *Bignonia tecomaeflora*, Rusby; E, Patelliform gland of *Bignonia impressa*, Rusby (in the figure the lower side of the leaf is directed upwards).—Original.

also of the second order. The branched hairs of *Tecoma alba*, Cham., *T. mollis*, H.B.K., and *T. ochracea*, Cham., exhibit a different type of structure, being more (*T. ochracea*) or less (*T. mollis*, Fig. 141, *A*) distinctly sympodial. Finally, the club-shaped hairs of *Zeyheria montana* exhibit a special type of structure; they have a uniseriate stalk and a head with ray-cells, which point in all directions. The glandular hairs agree with those found in the allied Orders in having heads divided by vertical walls only. Small capitate hairs are very common; they consist of a short unicellular stalk and a four-celled head, divided by four vertical walls, which form an ortho-

gonal cross (according to K. Schumann, these glands occur especially on the inner wall of the calyx, but also on the foliage leaves, e.g. in *Cuspidaria pterocarpa*, according to Hovelacque). Small scale-like glands (Fig. 141, *A–B*) are also of frequent occurrence; they have a stalk of a similar structure to that of the capitate glands, but their head is composed of a larger number of cells, and is divided by radial and sometimes also by tangential vertical walls; the cells of the head usually contain a secretion. According to O. Bachmann, such glands occur in species of *Amphicome, Amphilophium, Bignonia, Catalpa, Dolichandrone, Pithecoctenium* and *Tecoma*; according to Volkens in *Phyllarthron Bojeranum*, DC.; and according to Haberlandt in *Spathodea campanulata*, Beauv. It may be added, that the external glands of *Phyllarthron Bojeranum* cover the upper side of the leaf with a layer of varnish, that the glands of *Bignonia brasiliana*, Lam., and *Spathodea campanulata*, Beauv., function as water-excreting organs (hydathodes), according to Haberlandt, and that the glands of *Tecoma chrysantha*, DC., and *T. pentaphylla*, Juss., secrete carbonate of lime, according to O. Bachmann. External glands, in which the structure is analogous, but a considerable accumulation of secretion takes place between the cuticle and the cellulose-wall of the head, may be regarded as a modification of the glands just referred to; the accumulation of secretion causes the cuticle to be raised like a bladder. Glands with this structure have been observed by O. Bachmann in *Dolichandrone stipulata*, Benth. et Hook.; in *Bignonia calycina*, DC., *B. perforata*, Cham., *B. occidentalis*, Salzm., and *B. tecomaeflora*, Rusby (Fig. 141, *C–D*), they give rise to transparent dots in the leaf[1] (cf. DC., Prodr. ix, p. 160). Another type of gland is characteristic of the genus *Cremastus*, according to K. Schumann; here the uniseriate stalk is long, and its uppermost cell is differentiated as a short neck-cell, while the head is multicellular owing to vertical divisions, and has the shape of an inverted truncated cone; the secretion of these glands makes the surface of the organs on which they occur greasy. Glands of more complicated structure are: (*a*) those covering the young leaves of *Catalpa syringaefolia* in the bud, and persisting on the lower side of the pinnules in the mature leaf, where they occur in the angles formed by the lateral and main veins, and are visible to the naked eye as spots; they excrete sweetish nectar; and (*b*) the patelliform glands, which likewise excrete nectar, and have long been known to occur on the vegetative and reproductive organs of the Bignoniaceae. The glands of *Catalpa syringaefolia*, which form groups sunk in small depressions in the surface of the leaf, consist of a large stalk-cell seated on the epidermis, and a disc-shaped head composed of two layers of prismatic cells, which converge towards the stalk-cell, and have 4–6 angled outlines in surface-view (Reinke). The patelliform glands, which are very widely distributed[2] on the lower side of the leaves, and are generally visible to the naked eye as circular areas ½ mm. in diameter, have been examined in detail by Morini in *Bignonia grandiflora*, Spr., and *Tecoma radicans*, Juss., and by me in *B. impressa*, Rusby (Fig. 141, *E*). In the last of these species the glandular disc is separated by a groove from the rest of the epidermis in transverse section. The glandular disc consists of a layer of narrow cells elongated like a palisade, with small, polygonal, external surfaces. Below this lies a layer of low cells which are relatively large and polygonal in surface-view, and have those walls suberized which run at right angles to the surface of the organ. This layer of cells appears as a continuation of the epidermis, since, like the secretory palisade layer, it is of epidermal origin, as Reinke has shown in the case

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[1] Other transparent dots found in the leaf are caused by fissures in the mesophyll due to drying; they occur in *Spathodea campanulata*, Beauv. and *S. adenophylla*, DC. (Radlkofer).

[2] See Delpino, Mem. Accad. Bologna, 1888, p. 601 et seq.

of *Clerodendron fragrans*. Below these two layers there follows a third, distinctly differentiated layer. It is also to be observed that the patelliform glands are situated above an anastomosis of the veins, and that from the vascular bundles of the latter pitted (conducting ?) cells extend outwards towards the gland.

Oxalate of lime has been observed chiefly in the form of small octahedra, prisms, and small acicular crystals. Large solitary and clustered crystals are rare; the former occur in the cortical ring of stone-cells in *Tecoma pentaphylla*, Juss., according to Möller; the latter in the cortex of *T. pentaphylla*, and, according to Hovelacque, in the mesophyll of *Amphilophium Vauthieri*. Sphaero-crystals of undetermined organic composition (not phosphate of lime) have been found by Baccarini and Pirotta in alcohol-material of *Bignonia venusta*, Ker, and *Pithecoctenium clematideum*, Griseb.; Zimmermann met with nuclear crystalloids in the epidermis and mesophyll of the leaf in *Bignonia floribunda*, *Catalpa syringaefolia* and *Tecoma jasminoides*.

3. Structure of the Axis. The Bignoniaceae form a pronounced Order of lianes, and consequently **anomalies in the structure of the axis** are to be expected. These anomalies have been known for a long time, and have repeatedly formed the subject of investigation, the results of which have recently been summarized in an excellent manner by H. Schenck, and supplemented by his own observations. We meet with four kinds of anomalies in this Order. The first of these consists in the occurrence of wedges of bast in the xylem (Fig. 142, *A–B*); the second is the development of secondary zones of growth in the secondary cortex; the third is the formation of separate xylem-masses owing to fission (Fig. 142, *C*); and the fourth consists in the presence of inversely orientated bands of wood and bast at the margin of the pith. The first three anomalies are found almost exclusively in representatives of the Tribe Bignonieae, and sometimes more than one of these anomalies occurs in the same species (e.g. in *Doxantha capreolata*, Miers, where all three anomalies are met with simultaneously; the first anomaly is also found in the genus *Pandorea* (Tecomeae), whilst the fourth is met with in the genus *Campsis* (Tecomeae). In the two Tribes Jacarandeae [1] and Crescentieae, no anomalous structural features of the branch have hitherto been discovered.

I will now give an abstract of H. Schenck's account of the four anomalies (partly in his own words), beginning with the description of the wedges of bast in the xylem-mass (Fig. 142, *A–B*). Very young branches do not show this anomaly; they have a normal ring of vascular bundles, in which the xylem-ring contains vessels of small size only (axial wood of Strasburger). As soon as the periaxial wood (i.e. wood having vessels with wide lumina) appears, the formation of furrows commences, and follows a very definite law. The four furrows together form an orthogonal cross if we imagine them continued as far as the pith, and intersect one another at right angles. It is worthy of note that the furrows alternate with the orthostichies, the leaves being opposite in the cases under consideration. In some genera no more than four furrows are formed, but in other cases four secondary furrows appear between the original four; they do not penetrate so deeply into the wood as the latter, and they form angles of 45° with them. Bisecting the eight interspaces, eight additional (tertiary) furrows may be developed, and so on. Hence, if the formation of furrows continues to take place quite regularly, 4, 8, 16, 32, 64, &c., wedges of bast may be observed in transverse sections of the stem at successive stages. These wedges of bast are highly characteristic of many members of the Order. Similar structures, it is true, are also found

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[1] The statement in my 'Holzstruktur' regarding the occurrence of anomalous structure of the axis in *Jacaranda filicifolia*, Don has been shown to be incorrect by Radlkofer.

in other Natural Orders comprising lianes, e.g. in the Malpighiaceae, but the wedges of bast in the Bignoniaceae differ from them in two respects: firstly in their occurrence at regular intervals, and secondly in the fact that the cambium does not line the entire furrow, where the wedge of bast adjoins the wood (as in the other Orders), but is confined to the inner surface of the furrow, and is not present on the radial surfaces; cambium is also found on the external surface of the projecting portions of the wood. As a consequence of this peculiar distribution of the cambium, the wedges of bast must slide along the lateral surfaces of the furrows during growth in thickness, as has been pointed out by Mettenius, De Bary, and P. Schultz, and quite recently by H. Schenck, in reply to certain objections raised by Hovelacque. To facilitate this, fissures appear on the lateral surfaces of the furrows, but subsequently become closed again—a point which has also been observed in fresh material. The appearance of the wedges of bast in a transverse section of the stem may be of two kinds. In the simpler case the wedge appears of equal thickness throughout, and in transverse section is bounded towards the wood by a straight line on either side; in other cases, the line of separation between wood and bast is like a staircase

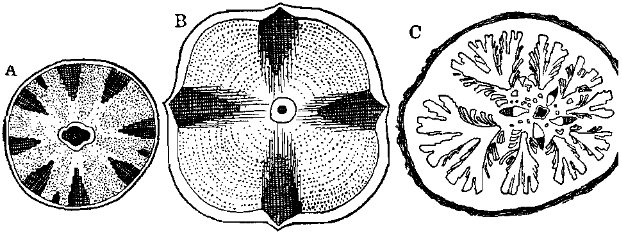

FIG. 142. Anomalous xylem-masses of certain Bignoniaceae: A, *Bignonia aequinoctialis* (Eggers, St. Thomas, Herb. Monac.) 1½ : 1; B, One of the Bignonieae, no. 633 in H. Schenck's collection of woods, nat. size; C, *Bignonia* spec. *catharinensis*, nat. size (H. Schenck, Wood-coll. no. 137).—A Original, B–C after H. Schenck.

(Fig. 142, *A–B*), owing to the successive step-like broadening of the bast-wedge as it approaches the periphery. In this case the transverse section has the form of a Maltese cross, and K. Schumann appropriately describes it by this name. The course of development is as follows. Small portions of the cambium, situated at the margins of the cambial strips which lie opposite the projections of the wood, suddenly begin producing a reduced amount of wood and a proportionally increased amount of bast; this takes place after the projecting portion of the wood has grown in thickness for some time in a normal manner by means of the entire strip of cambium bounding it externally; the same phenomenon is repeated at frequent intervals. Bast-wedges of the simple type, and four in number, are found in *Arrabidaea* and *Paragonia* [1], according to Bureau, as well as in *Callichlamys* (where secondary zones of growth also occur in older stems); according to Hovelacque, the formation of furrows also takes place in the three-year-old axis of *Pandorea jasminoides*, K. Sch., but the furrows here coincide with the four orthostichies of the leaves, this being contrary to what occurs in other Bignoniaceae with wedges of bast. Bast-wedges, four in number, and showing successive step-like enlargements, are mentioned by Bureau as occurring in *Adenocalymna*, *Cuspidaria*, *Fridericia*, *Petastoma*, *Pleonotoma*, *Stizophyllum*, *Tanaecium*, and *Tynanthus*. According to Bureau, wedges of

[1] Stems belonging to this type are also figured by H. Schenck (loc. cit.).

bast arising successively[1] (i.e. 4, 8, 16, &c., in number) are present in *Amphilophium*, *Anemopaegma*, *Clytostoma*, *Cydista*, *Lundia*, *Phryganocydia*, and *Pyrostegia*, and according to H. Schenck, in *Tynanthus elegans*, Miers; and finally, according to Bureau, in *Distictis*, *Glaziovia*, and *Haplolophium*, where this structure is, however, subsequently combined with the anomaly of successive rings of growth, and in *Bignonia*, *Doxantha* (*Anisostichus*), and *Melloa*[2], where it is combined with the anomaly of fission of the xylem-mass. A modification of the anomaly under consideration (that of wedges of bast in the wood) is found, according to Bureau, in the genus *Pithecoctenium*, in which the species *P. phaseoloides* (*Bignonia phaseoloides*, Cham.) has been investigated in detail by H. Schenck. Instead of having four wedges of bast arranged in the form of a right-angled cross, a transverse section of the axis shows four radial rows of bast-wedges similarly placed and connected by medullary ray-tissue. This type of structure originates in the following manner. At first the wood contains four wedges of bast, but during the further growth in thickness the strips of cambium opposite the projections of the wood and adjoining the bast-wedges become extended until they coalesce; they then enclose the four original bast-wedges by producing medullary ray-tissue at these places, and the cambium belonging to the bast-wedges ceases to divide; subsequently the formation of new wedges of bast takes place on the same radii, and so on. I may add that the structural features occurring in *Pithecoctenium* are also shown (*a*) by a liane from Southern Brazil, figured by Fritz Müller, and described as *Haplolophium*, in which, moreover, secondary zones of growth also appear in the cortex, and (*b*), according to Bureau, by stems of the genus *Distictis*, possessing 4, 8, 16, &c., bast-wedges, which arise successively and have a step-like structure.

The second anomaly occurring in this Order consists in the appearance of secondary zones of growth in the cortex. The genera showing this feature at first exhibit growth in thickness, accompanied by the formation of furrows as in the first type, but subsequently new strands of wood and bast arise in the secondary cortex (according to Van Tieghem in the pericycle), and grow in thickness by means of cambial tissue between the wood and bast. According to Bureau, the following genera exhibit this anomaly: *Callichlamys*, Miq., with four furrows of equal breadth in the original mass of wood, and additional zones of growth limited to one side of the stem; *Glaziovia*, Bureau, and *Haplolophium*, Cham.[3], both with successive formation of wedges of bast (4, 8, 16, &c.), in the central mass of wood, and concentric zones of growth in the cortex. Xylem-groups, arising secondarily in the secondary phloem, but not so well developed as in *Callichlamys*, &c., are found in *Doxantha capreolata*, Miers (according to Bureau and Jussieu), and in *Distictis*, Mart. (according to Bureau); in the last of these plants they lie opposite the furrows.

The third anomaly is that in which the mass of wood exhibits fission, and this can naturally only be observed in stems of sufficient age (Fig. 142, *C*). Wedges of bast are also originally present in the species exhibiting this anomaly. The subsequent fission takes place by dilatation and cell-division in the pith and in the parenchyma of the wood. Bureau states that this type is found in the following cases: (1) *Bignonia*, Bur.[4]; (2) *Doxantha capreolata*, Miers[5];

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[1] Compare also the stems of *Clytostoma* and of certain undetermined Bignonieae figured by H. Schenck, and the statements of Crüger and P. Schultz, cited by Schenck.

[2] Compare also Bureau's synopsis, which is given below at the end of the description of the anomalies (p. 608).

[3] See also H. Schenck, loc. cit., with regard to the liane, *Haplolophium*, examined by him and by Fritz Müller.

[4] For further statements in the literature with reference to this genus, see H. Schenck, loc. cit.

[5] Also according to Jussieu and De Bary.

(3) *Melloa*, Bur. According to K. Schumann (loc. cit., p. 200), *Parabignonia* and *Dolichandra* must 'probably' be added to these examples; and also *Macfadyena*, since in a more recent paper by H. Schenck (1895), the plant possessing the structure shown in Figs. 162 and 163 in his 'Lianenanatomie' (originally described as *Bignonia catharinensis*, and subsequently as *Bignonia exoleta*, Vell., by K. Schumann in the Natürliche Pflanzenfamilien, p. 200, note), is determined as *Macfadyena mollis* (Sond.), K. Sch., while the plant, of which the structure is figured by H. Schenck in Fig. 164 (originally described as *Bignonia unguis*), should probably be referred to *M. dentata*, K. Sch.

The fourth and last anomaly consists in the occurrence of two arcs of vascular bundles at the margin of the pith, showing inverse orientation of the wood and bast, as compared with the normal ring of bundles. This anomaly is characteristic of the genus *Campsis* with *C. radicans*, Seem. (*Tecoma radicans*) and *C. grandiflora* (Thunb.), K. Sch. (*Tecoma adrepens*). This has long been known in the case of *Campsis radicans* (Sanio), and in the second species it was observed by Hovelacque. Other species, formerly referred to the genus *Tecoma*, such as *T. capensis*, Thunb. (now = *Tecomaria capensis*, Fenzl), do not possess these medullary bundles. J. E. Weiss has shown that the medullary bundles of *Campsis radicans* are merely continuations of those of the normal peripheral ring, since the leaf-traces, after running through two internodes in the outer ring, curve into the pith at the next node, whilst undergoing a torsion through 180°. Hérail and Hovelacque dispute this statement, because, according to them, the development of the medullary bundles takes place at a relatively late stage.

Anomalies, similar to those of the axis, also occur in the root of the Bignoniaceae, as may be seen by reference to Schenck's summary on this subject. Frequently the same anomaly that occurs in the axis is repeated in the root (*Amphilophium paniculatum*, H.B.K., *Doxantha capreolata*, Miers, *Pyrostegia ignea*, Presl, having furrows in the wood of the root according to Avetta), but this is not so in other cases (species of *Campsis*, *Tecomaria*, and *Pithecoctenium* according to Avetta). The investigations on this point, however, are by no means complete, for the number of roots hitherto examined is far too small, and many of them were not sufficiently old. The occurrence of wedges of bast in the wood of the root is also mentioned by Crüger in the case of some species of *Bignonia*, and fission of the mass of wood by Bureau in swollen tuberous roots of *Bignonia unguis* and *B. Tweediana*.

To conclude the description of the anomalies I will follow the example set by De Bary and K. Schumann by reproducing Bureau's conspectus of the anatomical generic characters of the stems of the American Bignoniaceous genera (approximately in the words of De Bary's translation); in this review, moreover, not only the anomalies in the stem-structure are considered, but also special structural features presented by the wood, cortex and cork, as well as the shape of the entire stem.

A. Stem only possessing four wedges of bast.
- (*a*) Bast-wedges of uniform breadth, or showing uniform widening from within outwards.
  - (α) No new formation of fibrovascular tissue in the cortex.
    - I. Surface of cortex invariably provided with thin cork-tissue, even in old stems: *Arrabidaea*.
    - II. Surface of cortex, in old stems, with thick cork-tissue: *Paragonia*.
  - (β) Secondary formation of fibrovascular tissue in the cortex, giving rise to one-sided zones of growth: *Callichlamys*.
- (*b*) Bast-wedges (in the transverse section) widened externally in the form of steps.
  - (α) Stem cylindrical or angled, without grooves in the angles.
    - I. Cortex without stone-cells.
      - * Steps of the bast-wedges broad, i.e. of the width of several of the radial strips of wood, separated by small medullary rays.

1. Stem cylindrical or scarcely four-angled; bast-wedges remaining of uniform breadth for a long time, subsequently with high irregular steps: *Petastoma*.
2. Stem cylindrical, with delicate longitudinal furrows, subsequently thrown off; steps of the bast-wedges appearing late, broad and few in number: *Stizophyllum*.
3. Stem cylindrical, with four narrow furrows; bast-wedges broad; steps present at an early stage, and as broad or broader than their height: *Cuspidaria*.
4. Stem, at least when old, four-angled; cortex uneven with many lenticels; bast-wedges with regular steps, and broad medullary rays between the bands corresponding to the steps: *Tynanthus*.

** Steps narrow, i.e. not broader than the interspace between two medullary rays of the wood; stem cylindrical: *Fridericia*.

II. Cortex with stone-cells.

1. Stem somewhat flattened opposite the bast-wedges; bast-wedges short, only slightly widened; steps not broader than the interspace between two medullary rays of the wood; stone-cells scanty in the primary cortex, and scattered in the zone of the primary hard bast: *Tanaecium*.
2. Stem cylindrical; steps of the bast-wedges not numerous; a ring of stone-cells of several layers in the outer portion of the primary cortex: *Adenocalymna*.

(β) Young stem with four projecting ridges, corresponding to the bast-wedges, and containing bundles of mechanical tissue; the ridges are subsequently thrown off owing to cork-formation, and are replaced by distinct grooves; steps of the bast-wedges broad, irregular: *Pleonotoma*.

(c) Bast-wedges locally constricted owing to tangential extension of the production of wood; young stems octagonal with mechanical tissue in the angles; older stems, after these angles have been thrown off, cylindrical; cortex thick: *Pithecoctenium*.

B. Between the primary bast-wedges others arise; there are thus successively 4, 8, 16, 32, &c., bast-wedges in stems of different ages.

(a) Xylem-mass without subsequent formations, consequently remaining unaltered.

† Formation of secondary fibrovascular strands in the cortex does not take place.

(a) Young shoots cylindrical, without angles.

I. Stone-cells in the primary cortex and very numerous in the outer portion of the bast; bast-wedges with irregular steps: *Phryganocydia*.

II. Stone-cells wanting in the primary cortex.

* The first four bast-wedges long and narrow, the remainder short and broad; cortex with a red colouring matter: *Cydista*.

** All the bast-wedges alike; cortex without the red colouring-matter.

1. Stem twisted like a rope, with eight projecting, rounded edges; bast-wedges of successive ages differing little in length, all very narrow and with few steps, the first four having broad medullary rays in their outer portion: *Pyrostegia*.
2. Stem not twisted like a rope; wood very dense, with very narrow fibres and vessels; bast-wedges very numerous, with high, broad, irregular steps; medullary rays between the middle and the lateral lamellae of a bast-wedge, scarcely broader than the rest; pith very narrow: *Clytostoma*.
3. Stem not rope-like or scarcely so; wood loose, porous; steps of the bast-wedges very few; medullary rays between the middle and the lateral lamellae of a bast-wedge, strikingly broad; pith broad, the central portion disappearing: *Anemopaegma*.
4. Stem not rope-like; numerous bast-wedges with very narrow steps, and a broad medullary ray on either side of their middle lamella: *Lundia*.
5. Stem twisted like a rope; wood with large vessels; bast-wedges traversed tangentially at certain points by woody tissue;

occasionally (††) secondary formation of fibrovascular strands in the cortex opposite the bast-wedges: *Distictis.*

(β) *Young shoots with six edges formed by groups of mechanical cells, and subsequently thrown off, leaving a cylindrical stem*; cortex thin; numerous very unequal bast-wedges with irregular steps: *Amphilophium.*

†† Stem with concentric rings of growth arising in the cortex.

(α) Stem not twisted like a rope, or scarcely so; medullary rays of almost uniform breadth: *Haplolophium.*

(β) Stem twisted like a rope; medullary rays of very unequal breadth: *Glaziovia.*

(γ) Cf. *Distictis.*

(*b*) Internal portion of the wood split up by subsequent intercalary formations of parenchyma, wood and bast.

(α) Wood with annual rings; segments due to cleavage few; their bast contains bundles of wood, at first fan-shaped in transverse section, subsequently rounded off: *Doxantha.*

(β) Wood without annual rings; segments due to cleavage numerous, showing repeated fission, and with newly-formed parenchyma between them; the segments occupying the middle of the stem are turned in all directions.

1. Segments of the wood in the middle of the stem triangular, undivided, the remainder dichotomously divided: *Melloa.*
2. All the segments of the wood, the outer as well as the inner, dichotomously split: *Bignonia.*

In Bureau's review, as given above, we see that a number of the ordinary structural features of the wood and cortex are mentioned and employed systematically, such as the breadth of the medullary rays, width of the lumina of the xylem-vessels, the occurrence or absence of stone-cells and of bundles of sclerenchyma in the primary cortex. It now remains for us to give a short connected review of the general structural features of the wood and cortex, but it is necessary to point out that the results hitherto obtained in this direction are based on the investigation of very limited material.

In my 'Holzstruktur' I pointed out the following features on the basis of my investigation of only five representatives of the Order (*Doxantha capreolata*, Miers, *Pithecoctenium clematideum*, Griseb., *Catalpa Bungei*, C. A. Mey., *Tecomaria capensis*, Fenzl and *Jacaranda filicifolia*, Don). A transverse section of the **wood** shows medullary rays of no great breadth, and vessels with lumina of varied size (maximum diameter = ·036—·158 mm.[1]). The vessels in general have simple perforations; in the large vessels of *Campsis radicans*, reticulately perforated cross-walls occur side by side with simple perforations (Rodham). There are generally only bordered pits on the vessel-walls in contact with parenchyma of the medullary rays, but in *Catalpa Bungei* there are simple pits as well. Spiral thickening has been observed on the walls of the vessels and tracheids in *Doxantha capreolata*. The wood-prosenchyma bears simple pits, or pits with a small and indistinct border; septation of the lumen is to be found here and there in the species of *Doxantha*, *Pithecoctenium*, and *Tecomaria* mentioned above. According to Höhnel, tier-like structure of the wood occurs in *Bignonia brasiliana*, Lam., *B. chrysantha*, Jacq., and *Tecoma speciosa*, DC.; this depends on the arrangement of the medullary rays in tiers in the tangential section, and partly also on the mode of arrangement of the remaining elements of the wood. With regard to the structure of the **cortex**, the following statements may be made; they are chiefly derived from Möller's work. The cork generally develops immediately below the epidermis, e.g. in *Catalpa*, according to Sanio, in *Catalpa bignonioides*, Walt., *Jacaranda ovalifolia*, R. Br., *Oroxylum indicum*, Vent. (*Bignonia pentandra*, Lour.), and

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[1] Vessels having a diameter of as much as ·37 mm. have however been observed in the Order.

Crescentia Cujete, L., according to Möller; more rarely it arises somewhat deeper in the primary cortex, e.g. in *Tecoma*. The cork-cells always have wide lumina and usually have thin walls. The primary cortex is either collenchymatous, as in *Catalpa bignonioides*, or thin-walled, as in *Jacaranda ovalifolia*. In Bureau's review, reference has already been made to the presence of stone-cells, or sometimes of a ring of stone-cells in the primary cortex, and to the occurrence of sclerenchymatous strands in the same tissue in the angular branches of *Pleonotoma*, *Pithecoctenium*, and *Haplolophium*. At the outer limit of the phloem there are groups of primary hard bast, which vary in the extent of their development, but a composite and continuous sclerenchymatous ring is never present. The secondary bast shows a tendency to be stratified into hard and soft bast. A similar stratification is found in the bast-wedges in the wood, and these portions of the phloem are further distinguished by the possession of sieve-tubes with very wide lumina.

According to Mentovich, the pith is homogeneous in *Campsis radicans*, where, unlike the pith of most tropical Bignoniaceae, it consists of unlignified cells.

Literature: Jussieu, Monogr. des Malpighiacées, Paris, 1843, p. 119.—Mettenius, Bau der Bignonien, Linnaea, Bd. xix, 1846, p. 567.—Crüger, in Bot. Zeit. 1850, p. 108.—Bureau, Monogr. des B. etc., Paris, 1864, pp. 120 and 161 et seq.—Sanio, in Bot. Zeit. 1864, pp. 61 and 228.—Fritz Müller, Kletterpfl., Bot. Zeit. 1866, p. 66 and Tab. iii.—Bureau, Caractères tirés de la struct. de la tige pour la classif. des B., Bull. Soc. bot. de France 1872, pp. 14–20.—Martinet, in Ann. sc. nat., sér. 5, t. xiv, 1872, pl. 12.—Möller, Holzanat., Denkschr. Wiener Akad. 1876, pp. 60–1 and 356.—Reinke, in Pringsheim Jahrb., Bd. x, 1876, p. 153 and Tab. xii.—De Bary, Vergl. Anat., 1877.—Möller, Rindenanat., 1882, pp. 183–9.—J. E. Weiss, Markst. Gefässbündelsyst., Bot. Centralbl. 1883, iii, pp. 293 and 318 et seq., Tab. i.—Höhnel, Stockwerkart. aufg. Holzk., Sitz.-Ber. Wiener Akad., Bd. lxxxix, Abt. 1, 1884, p. 41.—Johow, in Pringsheim Jahrb., Bd. xv, 1884, p. 309.—P. Schulz, Anom. Dickenwachst. v. *Bignonia aequinoctialis*, Flora 1884, pp. 198–204.—Vesque, Gamopétales, Ann. sc. nat., sér. 7, t. i, 1885, pp. 317–26.—Hérail, in Ann. sc. nat., sér. 7, t. ii, 1885, pp. 255 and 279 et seq., pl. 19–20.—Mentovich, Mark, Klausenburg, 1885, Hungarian; abstr. in Just. 1885, i, p. 789.—Solereder, Holzstr., 1885, pp. 195–7.—O. Bachmann, Schildh., Flora 1886, sep. copy, pp. 26–7 and Tab. ix.—Morini, Nett. estranuz., Mem. Accad. Bologna 1886, p. 355 and tav. iv.—Pirotta, Sferocristalli del *Pithecoctenium*, Ann. dell' Ist. bot. di Roma, 1886, 16 pp.—Radlkofer, in Sitz.-Ber. Münch. Akad. 1886, p. 3 note and p. 325.—[Avetta, Anomalie di struttura nelle radici etc., Ann. dell' Ist. bot. di Roma 1887, p. 7.]—Hovelacque, Coins libériens des B., Compt. rend., t. cv, 1887, 4 pp.—Petit, Pétiole, Mém. Soc. sc. phys. et nat. de Bordeaux, sér. 3, t. iii, 1887, pp. 351–2 and pl. vi.—Baccarini, Sferocristalli, Malpighia, vol. ii, 1888, pp. 1–9.—Hovelacque, Caract. anat. généraux de la tige des B., Bull. Soc. d'études scientif. de Paris, T. xi, 1888, 7 pp., and Appareil végétatif des B. etc., Paris, 1888, pp. 5–373.—Douliot, Périderme, Ann. sc. nat., sér. 7, t. x, 1889, pp. 381–2.—Volkens, Lack. Bl., Sitz.-Ber. deutsch. bot. Gesellsch. 1890, p. 130.—Rodham, Gefässquernetze, Sitz.-Ber. deutsch. bot. Gesellsch. 1890, p. 188 et seq.—Ross, Periderma, Malpighia, vol. iv, 1890–1, p. 97.—Zimmermann, Pflanzenzelle, 2. Heft, 1891, p. 137.—H. Schenck, Anat. d. Lianen, 1893, pp. 212–37 and 254 et seq., Tab. xi–xii.—K. Schumann, in Natürl. Pflanzenfam., iv. Teil, Abt. 3b, 1894, pp. 193–204.—Haberlandt, Trop. Laubbl. II, Sitz.-Ber. Wiener Akad., Bd. ciii, Abt. 1, 1894, p. 528 et seq. and Tab. ii.—Loesener, in Bull. de l'Herbier Boissier, vol. iii, 1895, p. 619 and pl. 17.—H. Schenck, Zerklüftungsvorg., Jahrb. f. wiss. Bot., Bd. xxvii, 1895, pp. 604–7.—Bureau and Schumann, in Flora brasil. viii, 2, 1896–7, pp. 6 to 10 and Tab. 70, 71 and 112.—[Hill, Roots of *Bignonia*, Ann. of Bot. 1898.]

PEDALINEAE.

This small Order is almost entirely composed of herbaceous species. It is distinguished anatomically by two characters, viz. the lack of a special type of stoma, and the occurrence of glandular hairs, the heads of which are invariably divided by vertical walls only, but in other respects vary in differentiation and shape. Oxalate of lime, when present, is excreted in the form of small bodies resembling clustered crystals, and in that of small solitary crystals (e. g. abundantly in the mesophyll of *Martynia diandra*, Glox., or *Rogeria adenophylla*, Gay); more rarely (in the axis) it occurs in the form of large clustered or solitary crystals. The structure of the wood in the species investigated (*Pedalium* sp., Hildebrandt, n. 3406, Madagascar; *Rogeria adenophylla*, Gay; *Sesamum indicum*, L.) shows: (*a*) either no broad medullary rays, or rather

broad rays here and there only; (*b*) vessels with rather large lumina (diameter as much as ·06 mm.), simple perforations, and bordered pits in contact with parenchyma; and (*c*) wood-prosenchyma, with relatively wide lumina, and bearing simple pits.

Amongst the glandular **trichomes** we must specially describe the mucilage-hairs (Fig. 143), which were first discovered by F. W. Oliver in the genera *Trapella, Pedalium,* and *Pretrea,* and, according to Stapf, are probably characteristic of the whole of his Family Pedaliaceae. This includes the Tribes Pedalieae, Sesameae and Pretreae of Bentham and Hooker, and also the genus *Trapella,* but excludes the Tribe Martynieae. In the literature, however, only *Pedalium, Josephinia, Pretrea* and *Trapella* have been actually described as possessing mucilage-hairs; to these I can add *Sesamum* (*S. indicum,* L.), *Rogeria* (*R. adenophylla,* Gay), and *Ceratotheca* (*C. melanosperma,* Hochst.) from my own investigations. The mucilage-glands in question are capitate hairs, the stalk being usually represented by a single short cell, although it may exceptionally (e.g. in *Rogeria adenophylla* on the veins of the leaf) be longer and multicellular; the head is peltate, and consists of four (in isolated cases also of 5–8) cells, which are arranged like a cross, their walls projecting convexly at the margin of the head. The mucilage, contained in the cells of the head and occupying the greater part of the lumina, arises by the metamorphosis of the cellulose-walls, which are covered by a delicate cuticle; in the mature and functional gland the lumen of the glandular cells is represented by quite a small space, which is filled with the remains of the protoplast. The shortly stalked mucilage-hairs are sometimes present in such large numbers on the lower side of the leaves, that the surface appears to be covered with white grains. In addition to mucilage-hairs, *Sesamum indicum* and *Ceratotheca melanosperma* possess glandular trichomes of a different type, viz. hairs with a long uniseriate stalk and a spherical or turbinate head; the stalk is generally composed of long cells at the base graduating into shorter cells above; while the head is divided by one or a few vertical walls into cells resembling a palisade in side-view. Similar glandular hairs with long stalks are met with amongst the Martynieae (in which no mucilage glands are present), in the species *Martynia diandra,* Glox., and *Craniolaria annua,* L.; in the latter plant the glandular heads are distinguished by having a relatively large number of palisade-cells and a depressed apex. Other external glands with a short, unicellular stalk, but with a head of the same structure as in the glands with long stalks, are found in *Martynia* and *Craniolaria.* Clothing hairs, in the form of usually long, uniseriate trichomes with wide lumina, have been observed on the leaf in *Martynia diandra, Craniolaria annua, Sesamum indicum,* and *Ceratotheca melanosperma;* hairs with a verrucose surface and wide lumina and mostly composed of one, more rarely of two, cells are found on the upper side of the leaf in *Rogeria adenophylla.*

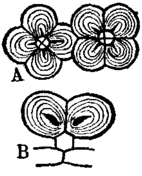

FIG. 143. Mucilage-hair of *Sesamum indicum,* L.—Original.

We may add the following statements regarding the **stomata.** In most of the species investigated (*Martynia diandra, Pedalium* sp., *Rogeria adenophylla, Sesamum indicum*) the stomata are found on both sides of the leaf, but in *Craniolaria annua* only on the lower side. The submerged leaves of *Trapella sinensis,* Oliv., bear no stomata, but the deltoid floating leaves of the same species develop stomata on the upper side (Oliver). Each pair of guard-cells is generally surrounded by an indefinite number of ordinary epidermal cells; but sometimes (upper side of the leaf in *Rogeria adenophylla*) three subsidiary cells are more or less distinctly differentiated. In *Trapella*

the leaves of both types possess peculiar water-pores in the form of small openings, which are situated in the indentations between the crenations of the margin, and arise by the separation of epidermal cells; beneath the water-pores there are terminations of vascular bundles, provided with an epithema of small cells (Oliver).

I may add a few remarks to the statements made above regarding the structure of the **axis**. The pith of *Pedalium* sp. shows septation without sclerosis. 'In the pericycle sclerenchymatous groups composed of bast-fibres (*Sesamum indicum*), or of bast-fibres and stone-cells (*Rogeria adenophylla*) are sometimes present; in *Pedalium* sp. there is no sclerenchyma in the pericycle. The formation of cork has only been observed in *Pedalium* sp., where it takes place subepidermally. Regarding the aquatic plant *Trapella*, Oliver mentions that the stem contains a small centrally placed vascular cylinder, which encloses a pith consisting of a few cells, and is separated from the lacunar cortex by an endodermis.

Literature: Martinet, in Ann. sc. nat., sér. 5, t. xiv, 1872, p. 155 and pl. 13.—F. W. Oliver, *Trapella*, Ann. of Bot., vol. ii, 1888, pp. 75–115 and pl. v–ix.—Stapf, in Natürl. Pflanzenfam., iv. Teil, Abt. 3 b, 1895, pp. 254 and 267.

ACANTHACEAE.

1. Review of the Anatomical Features. The following anatomical characters may be said to be common to the members of this Order: (*a*) a uniform type of stoma, the stomata being invariably accompanied by subsidiary cells, which are placed transversely to the pore (Fig. 144, *A*); (*b*) the occurrence of glandular hairs, in which the head is either panduriform and bicellular, owing to the presence of a vertical wall (Thunbergieae), or disc-shaped, and then unicellular or multicellular with vertical walls (see Fig. 144, *B* and *D*); (*c*) simple perforations in the vessels, narrow medullary rays, and wood-prosenchyma bearing simple pits and sometimes septate. Cystoliths are very widely distributed, and are characteristic of certain divisions of the Acanthaceae; their shape as well as their occurrence in definite tissues of the leaf (epidermis or mesophyll), may be employed for the purposes of detailed classification within the Order (see Fig. 144, *C–J*). Oxalate of lime is excreted in the form of small prismatic or acicular crystals. In addition to the glandular hairs, clothing hairs are present, and are, for the most part, of the ordinary simple unicellular or uniseriate type; special forms of trichomes, such as unicellular, two-armed hairs (sect. *Somalia* of the genus *Barleria*) or candelabra-hairs (species of *Barleria*, *Ruellia discifolia*, Oliv.), are rare. In the bast, in many members of the Order, there are cells with wide lumina, filled with acicular fibres (raphidines), which have hitherto only been observed in this Order (see Fig. 146). Finally, in a number of species the stem possesses anomalous structure. The species of *Acanthus* have vascular bundles at the margin of the pith, with the wood and bast inversely orientated. Among the Barlerieae the genera *Barleria* (incl. *Somalia*), *Barleriola*, *Lepidagathis*, *Lophostachys* and *Neuracanthus*, and probably also *Glossochilus* and *Volkensiophyton* are distinguished by the occurrence of intraxylary and interxylary phloem. Intraxylary phloem alone occurs in *Nelsonia*, interxylary phloem alone in certain species of *Thunbergia*. Another group of species belonging to *Thunbergia* exhibits wedges of soft bast, and these are either given off internally by the cambium, and subsequently appear as interxylary phloem owing to their enclosnre in the wood during the growth in thickness of the branch, or they are of the same nature as the wedges of soft bast in the Malpighiaceae. In conjunction with the occurrence of wedges of soft bast, a subsequent fission of the wood takes place in a few species of *Thunbergia*,

in *Mendoncia* (Fig. 148), and *Afromendoncia*, and possibly also in *Pseudocalyx*; further in these species of *Thunbergia*, *Mendoncia*, and *Pseudocalyx* secondary masses of wood and bast arise at the margin of the pith.

2. Structure of the Leaf. The leaf-structure of the Acanthaceae has been little investigated. Only special features, chiefly the cystoliths and the hairy covering, have formed the subject of more extensive investigations.

Vesque describes bifacial leaf-structure in the species examined by him. The **stomata** either occur only on the lower side of the leaf, or on both sides; they probably follow the Caryophylleous type in all cases, the pairs of guard-cells being accompanied by two or more subsidiary cells, which are placed transversely to the pore, and are cut off by similarly placed division-walls before the differentiation of the mother-cell of the stoma (Fig. 144, *A*). Gelatinization of the epidermis of the leaf has not been observed. A **hypoderm** composed of one or two layers of large cells is found in *Acanthus ilicifolius*, L., according to Schimper. Special **internal secretory organs** are not known with certainty to occur in the leaf, or in the other organs. Russow's statement regarding the presence of intercellular canals filled with a secretion in the root of *Rhinacanthus communis*, and in the root, stem and leaves of *Justicia picta*, requires confirmation.

Oxalate of lime, when present, is excreted in the form of small crystals which may be acicular, prismatic, or of other shapes. In the leaf it is found in all parts of the mesophyll, and commonly also (e. g. *Aphelandra*, *Dilivaria*, according to Vesque) in the epidermis, or (*Ruellia formosa*, according to Vesque) in the hairs; in the axis it occurs in the pith, the medullary rays of the wood and bast, and in the primary and secondary cortex.

The **hairy covering** consists of clothing and glandular hairs. The clothing hairs are usually simple and either unicellular or uniseriate. Hobein states that in most of the Barlerieae investigated by him there are unicellular hairs with thick walls and a narrow canal-like lumen having a spherical enlargement at the base of the hair; in *Lepidagathis*, which belongs to the same group, uniseriate hairs with unthickened walls occur as well, whilst in *Barleriola* and *Neuracanthus* unicellular hairs are wanting. The same author describes long uniseriate hairs with strongly thickened walls as occurring in the Aphelandreae (with the exception of *Stenandrium*); these hairs consist of a few short basal cells and a long terminal cell. According to Hobein, the Acantheae have short unicellular or bicellular hairs, the walls of which are little if at all thickened; more rarely long, uniseriate hairs with walls showing the same features are found in this Tribe. Trichomes of the latter type are also met with in the remaining members of the Order. In *Thunbergia* (*T. fragrans*, Roxb.) the uniseriate hair springs from the middle of a group of basal cells, which are silicified. Special forms of clothing hairs are rare. The following are examples: (*a*) the unicellular, two-armed hairs, characteristic of the section *Somalia*, Lindau, of the genus *Barleria*; (*b*) the candelabra-hairs of *Barleria Hildebrandtii*, Moore, in which the component tiers are as a rule formed by two cells lying side by side; (*c*) the trichomes of *Barleria longiflora*, L.f. (according to Radlkofer), which resemble the candelabra-hairs; and (*d*) perhaps also those of *Ruellia discifolia*, Oliv. (see Hooker Ic., Tab. 1511). Glandular hairs are perhaps of general occurrence in the Order. They are, for the most part, small and shortly stalked, though glandular hairs with long stalks occur on the floral organs, according to Lindau. According to the shape of the head two types of hairs may be distinguished. In the first type the head is panduriform, and divided into two cells by a vertical wall at right angles to the longest diameter (Fig. 144, *B*). In the second type the glandular head is disc-shaped, and either unicellular, or composed of a varying number of cells separated by vertical walls (Fig. 144, *D*). According to Hobein, the

panduriform glands are characteristic of the Thunbergieae, whilst the disc-shaped glands occur in the rest of the Acanthaceae. According to Volkens,

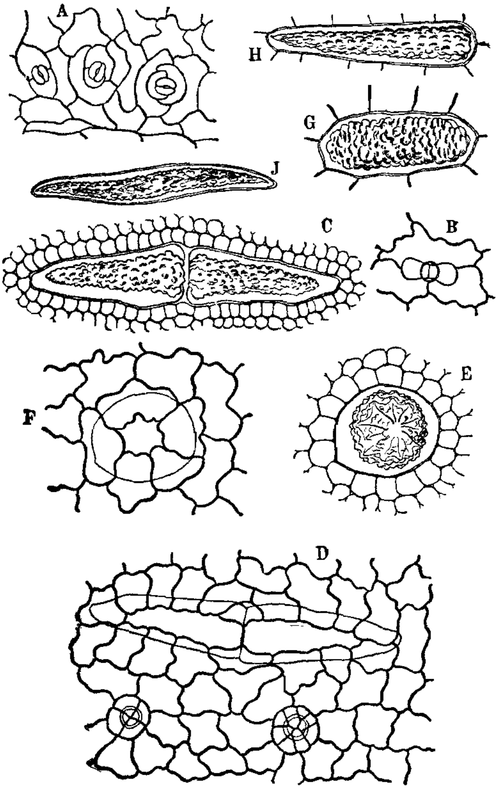

FIG. 144. A, Type of stoma found in the Acanthaceae. B, Glandular hair of *Thunbergia fragrans*, Roxb. C, D, *Barleria Prionitis*, L.: C, *Double cystoliths with the cells containing them*, and the surrounding palisade-tissue seen from the surface at a low focus; D, Portion of the epidermis of the leaf of the same plant, the cystoliths being omitted. E-F, *Asystasia scandens*, Hook.: E, *Cystolith with the cell containing it*, as in C; F, Portion of the upper epidermis of the leaf with a lithocyst, as in D. G, Cystolith of *Justicia Ecbolium*, L. H, Cystolith of *Stephanophysum angustiflorum*, Nees. J, Cystolith of *Sanchezia macrocnemis* (Nees).—Original.

in *Petalidium linifolium*, Anders., the secretion of the disc-shaped glands covers the leaves with a layer of varnish.

Besides investigating the hairy covering, Hobein made a detailed examination of the distribution of the **cystoliths** in the leaf of the Acanthaceae. Certain divisions of this Order do not possess cystoliths, whilst others are distinguished by their presence, and may be characterized in some cases in a very satisfactory manner by the place of occurrence or the special shape of the cystoliths. Hobein's table, which briefly summarizes the results of his investigations in this direction, is given below, and is followed by a few remarks of a more general nature on the cystoliths of the Acanthaceae. The system of classification, followed in the table and throughout Hobein's work, is that of Bentham and Hooker, with a few emendations introduced by Radlkofer.

I. Cystoliths not present: Thunbergieae [1], Nelsonieae [2], Acantheae [3], Aphelandreae [4].

II. Cystoliths always present:

1. Cystoliths never contained in epidermal cells of the leaf, but always present in the subepidermal tissue: *Anisotes trisulcus*, Nees, *Adhatoda vasica*, Nees, *Harpochilus phaeocarpus*, Nees.

2. Cystoliths always present, but only in epidermal cells of the leaf; not present in the subepidermal tissue:

   A. Double cystoliths [5], i.e. two rounded or elongated cystoliths belonging to two neighbouring epidermal cells; the ends of the cystoliths, which are often thickened in the form of a club, are turned towards one another (Fig. 144, *C–D*): Barlerieae pro parte, viz. *Periblema*, *Crabbea* and *Barleria*, which almost without exception have double cystoliths, and *Lophostachys* and *Barleriola*, which possess both double and simple cystoliths, the former in smaller numbers; also *Lepidagathis terminalis*, Hochst., *L. glandulosa*, Nees, and *L. scariosa*, Nees, with simple and double cystoliths.

   B. Cystoliths always lying singly:

   (*a*) Round cystoliths (Fig. 144, *E–F*), and in rare cases transitions to elongated forms, which are blunt at both ends: Asystasieae pro parte, viz. *Asystasia*, Pseuderanthemeae [6], Andrographideae [7].

   (*b*) Elongated cystoliths with blunt extremities, more rarely round cystoliths (Fig. 144, *G*): Eujusticieae, pro parte, viz. *Monothecium*, *Haplanthera*, *Glockeria*, *Schwabea*, *Justicia* (with *Hemichoriste*, *Gendarussa*, *Monechma*, *Amphiscopia*, *Rhaphidospora*, *Anisostachya*), *Siphonoglossa*, *Beloperone*, *Isoglossa Leptostachya*, *Rhytiglossa* (with transitions to the cystoliths of the type given under C), *Anisotes*, *Adhatoda*, *Rhinacanthus*, *Cyrtanthera*, *Sericographis*, *Libonia*, *Harpochilus*, *Schaueria*, *Graptophyllum* and *Thyrsacanthus*; also *Lepidagathis*, *Lophostachys* and *Barleriola* (see above II, 2 A).

   (*c*) Elongated cystoliths, which are always distinctly pointed at one end (Fig. 144, *H*): *Neuracanthus* (but the form of the cystoliths in this case is not typical); *Chamaeranthemum* and *Herpetacanthus* (Asystasieae); Eujusticieae pro

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[1] Species of *Hexacentris*, *Meyenia*, *Thunbergia*, *Mendoncia* and *Pseudocalyx* have been examined; it is a very noteworthy fact that, according to Roulet (loc. cit., p. 264), *Thunbergia reticulata*. Hochst., has cystoliths in the epidermis of the branch, a point which requires further investigation.

[2] Species of *Elytraria*, *Nelsonia*, *Ebermaiera* (with *Erythracanthus*) have been examined.

[3] Species of *Blepharis* (with *Acanthodium*), *Acanthus* (with *Cheilopsis* and *Dilivaria*) and *Crossandra* have been examined.

[4] Species of *Aphelandra* (with *Strobilorhachis* and *Lagochilium*), *Geissomeria* (with *Salpixantha*) and *Stenandrium* have been examined.

[5] Sometimes one also meets with cystoliths in fours (e. g. in species of *Barleria*).

[6] Species of *Pseuderanthemum*, *Anthacanthus*, *Codonacanthus* and *Cystacanthus* have been examined.

[7] Species of *Andrographis* (with *Erianthera*), *Haplanthus*, *Gymnostachyum* (with *Cryptophragmia*) and *Phlogacanthus* have been examined.

parte, viz. *Jacobinia* (with *Pachystachys*), *Habracanthus* and *Chaetothylax*; Ruellieae pro parte[1], viz. *Spirostigma*, *Stephanophysum*, *Echinacanthus*, *Phaylopsis*, *Blechum*, *Pentstemonacanthus*, *Daedalacanthus* and *Trichanthera*.

(*d*) Elongated cystoliths, which are pointed at both ends (Fig. 144, *J*): *Sanchezia* (of the Ruellieae), *Rostellularia* (of the Eujusticieae).

(*e*) Cystoliths of varying shape: Ruellieae pro parte[2], Dicliptereae[3].

The foregoing table facilitates the recognition of the different features connected with the shape of the cystoliths found in this Order, and also indicates the seat of their occurrence in the leaf. In the axis cystoliths occur in all the tissues, with the exception of the wood. Those in the leaf are generally recognizable with the naked eye or more easily with a lens; in herbarium-material they appear as small striae or dots when viewed by reflected light. When the cystoliths do not occur in the epidermis, but belong to the mesophyll, it is not possible to recognize them in this way, but they sometimes (*Anisotes trisulcus*, Nees, and *Harpochilus*, according to Hobein) give rise to transparent dots in the leaf. As regards the mode of attachment of the foliar cystoliths to the cell-wall it has only rarely been possible to demonstrate the presence of slender stalks in herbarium-material, and it is not improbable that the thin stalks of the cystoliths may be resorbed at an early stage. Hobein carefully examined the cystoliths situated in the epidermis from this point of view. In the rounded cystoliths or in those of elongated shape with blunt extremities, usually only a small portion of the (epidermal) lithocyst takes part in the formation of the leaf-surface, and it is to this part of the cell that the stalk of the cystolith is attached. The spindle-shaped cystoliths, which are pointed at both ends, likewise have a slender stalk, inserted centrally and attached to the small rounded portion of the wall of the lithocyst, which reaches the surface of the leaf. In the elongated cystoliths, with one pointed and one blunt end, the point of attachment is at the blunt end; in this case the stalk is not attached to the outer wall of the lithocyst, which has a relatively large surface, but to one of the lateral walls. The double cystoliths of the Barlerieae are always attached to the wall separating the two lithocysts. With regard to the chemical nature of the cystoliths, it may be mentioned that, as a rule, the skeleton consists of pure cellulose, and that sometimes (e.g. in *Ruellia japonica*, Thunb.) the internal portion of the cystolith is silicified; a strong incrustation of carbonate of lime is usually present. Hobein mentions the occurrence of cystoliths devoid of lime in the subepidermal tissue of the leaf in *Harpochilus*, and the same feature is described by Radlkofer in *Cystacanthus turgida*, Nichols., where the cystoliths give rise to transparent dots in the leaf, and by Molisch as a constant occurrence in the pith of *Goldfussia isophylla*, Nees, *G. glomerata*, Nees, and *Ruellia ochroleuca*. The non-calcified cystoliths of *Goldfussia* and *Ruellia* are found in certain elongated cells of the pith; they are very long, and are specially distinguished by the fact that they consist of slightly lignified cellulose, and are connected with the cell-wall by numerous stalks (Fig. 145). Before leaving the subject of cystoliths we may mention that in the pith of *Fittonia argyro-*

[1] In his concluding table Hobein also mentions *Dyschoriste* under this heading; on p. 428 of his work however only *Spirostigma*, *Stephanophysum* and *Echinacanthus* among the Euruellieae are mentioned as having oblong cystoliths, pointed at one end.

[2] The species of the following genera investigated by Hobein belong to this class: *Adenosma*, *Hygrophila*, *Asteracantha*, *Hemiadelphis*, *Physichilus*, *Polyechma*, *Nomaphila*, *Brillantaisia*, *Calophanes*, *Linostyles*, *Chaetacanthus*, *Ruellia*, *Dipteracanthus*, *Cryphiacanthus*, *Eurychanes*, *Stemonacanthus*, *Siphonacanthus*, *Arrhostoxylum*, *Homotropium*, *Hemigraphis*, *Stenosiphonium*, *Strobilanthes*, *Endopogon*, *Phlebophyllum*, *Goldfussia*, *Calacanthus*.

[3] Species of *Clistax*, *Rungia*, *Dicliptera*, *Peristrophe* and *Hypoestes* have been examined.

neura, Hort. and *F. Verschaffeltii*, Hort., K. Richter observed cystoliths of very irregular form, some being antler-shaped, others helicoid.

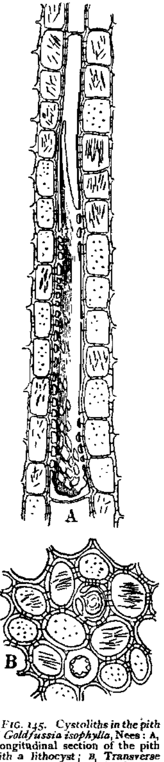


FIG. 145. Cystoliths in the pith of *Goldfussia isophylla*, Nees: A, Longitudinal section of the pith with a lithocyst; B, Transverse section through the pith with two lithocysts cut transversely; there are also small acicular crystals in the cells of the pith.—Original.

We may now describe the **acicular fibres** (raphidines, Fig. 146, *A–B*) which were first observed by Russow in certain members of the Order, and were subsequently described by Vesque, Radlkofer, and Roulet; so far they have not been found in any other Order of plants, nor have detailed investigations as to their distribution in the Acanthaceae been undertaken. These acicular fibres are rather long fibrous cells, with thick walls and narrow lumina; they are pointed at both ends, and are small in cross-section. Like raphides they are found in varying numbers—sometimes accompanied by fibres of greater diameter—united in the form of a bundle, which lies inside a large cell of corresponding shape; according to Russow and Roulet the bundle of fibres is derived from the cell containing it by cell-division. They lie freely in the cavity of this cell, since the primary lamellae of the acicular fibres become resorbed during their development; in case of injury to the mother-cell enclosing them, they emerge separately in the same way as the raphides of a ruptured raphide-sac. These bundles of acicular fibres are found in the bast (as a rule both in stem and root), in the petiole, and in the veins of the leaf. In many cases a simple incision of the veins of the leaf is sufficient in order to obtain at once a large quantity of acicular fibres. They are sometimes present in very great abundance, but in other cases it is difficult to demonstrate their presence owing to their small numbers.

Russow first met with these structures in *Hexacentris coccinea*; the same author also describes acicular cells as occurring in species of *Ruellia*, in *Sanchezia* '*picta*'[1] (in the stem), *Fittonia gigantea* and *Aphelandra aurantiaca* (only in the root), *Hexacentris mysorensis* (only in the petiole), while they are stated to be absent in *Aphelandra cristata* and *Eranthemum*. Vesque has demonstrated their presence in *Cyrtanthera catalpaefolia*, *Meninia turgida*, *Adhatoda ventricosa* and *Fittonia*; Roulet found them in all the numerous species of the genus *Thunbergia* which he examined, though not in equal abundance in all cases, nor always in all the organs of any one species; finally, they were observed by Radlkofer in *Thunbergia*, *Pseudocalyx* and *Mendoncia*.

The **petiole** has only been examined in detail in *Thunbergia alata*, Bojer and *Acanthus mollis*, L. According to Petit the principal fibrovascular system in the characteristic region consists of a ring of vascular bundles in both cases; in addition to this ring, 1–3 isolated bundles occur on each side of the petiolar groove. Plitt mentions the occurrence of an open fibrovascular arc, composed of one or more vascular bundles, in the species which he investigated belonging to the genera *Aphelandra*, *Cyrtanthera*, *Dipteracanthus*, *Fittonia*, *Gendarussa*, *Peristrophe*, *Sanchezia*, *Schaueria*, *Strobilanthes* (*Ruellia maculata*, Wall.) and *Whitfieldia*.

[1] Anne sphalmate ex '*Justicia picta*'?

3. Structure of the Axis. Considering the large size of the Order, the structure of the axis also has been very little investigated. The following statements regarding the structure of the **wood** are based on my own investigation of species of the genera *Mendoncia, Ruellia, Strobilanthes, Blepharis, Crossandra, Lepidagathis* and *Barleria*, and Roulet's work on *Thunbergia*. The size and arrangement of the vessels vary; the lumina are of very considerable size in the lianes. The medullary rays are not broad, being one, two, or at the most three cells in breadth; the cells are frequently elongated in the vertical direction. In most of the investigated species there are bordered pits on the vessel-wall, even where it is in contact with parenchyma; *Mendoncia pilosa*, Mart. forms an exception, for in this species bordered and simple pits, with intermediate forms, occur at these points. The perforations of the vessels are simple. Wood-parenchyma is never

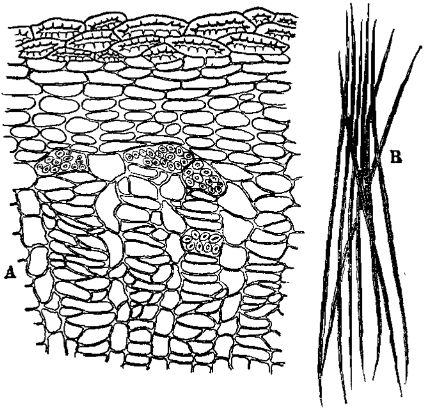


Fig. 146. The raphidines or acicular fibres of the Acanthaceae: A, Transverse section through the inner portion of the cortex (pericycle and bast) in *Adhatoda ventricosa*, Nees, showing the bundles of acicular fibres in transverse section; B, Group of acicular fibres from the leaf of *Thunbergia cerinthoides*, Radlk., obtained by making an incision into the lower surface of the leaf.—Original.

developed in abundance. The wood-prosenchyma appears to have simple pits; septation of the lumina has been observed in species of *Mendoncia, Ruellia, Strobilanthes* and *Lepidagathis*. Tracheids sometimes (*Thunbergia*) occur accompanying the prosenchyma, but in smaller numbers.

We know even less of the structure of the **cortex** than of that of the wood, apart from the occurrence of acicular fibres in the bast, as mentioned above. Our whole knowledge of the subject is practically limited to an investigation of the genus *Thunbergia* by Roulet. A very characteristic feature of almost all the species of *Thunbergia* is the presence of a hypoderm, consisting of fibrous cells, and lying beneath the epidermis of the stem. According to Roulet a similar hypoderm occurs in other genera of the group

Thunbergieae, viz. in *Monachochlamys* and *Mendoncia*. This fibrous hypoderm shows varied differentiation in the species of the genus *Thunbergia*, and may be employed for systematic purposes. Thus it may either form narrow tangential bands one or two cells in thickness (*Meyenia Hawtayniana*, Nees, and *M. longiflora*, Benth., *Thunbergia fragrans*, Roxb., *T. alata*, Boj., &c.), these bands being mostly quite continuous and only locally interrupted by collenchyma; or it may consist of bundles which are more strongly developed in the radial direction (*T. grandiflora*, Roxb., *T. Cycnium*, Moore, *T. gentianoides*, Radlk.); in *T. cerinthoides*, Radlk. and *T. Fischeri*, Engl. transitional types occur, whilst in *T. angolensis*, Moore, groups of stone-cells are present in place of the fibrous hypoderm. The development of periderm takes place superficially in *Thunbergia*, viz. on the inner side of the fibrous hypoderm; it may be added that according to Tchouproff the phellogen arises in the epidermis in *Ruellia*, and in the endodermis in *Aetheilema*. In *Thunbergia angolensis*, Moore, stone-cells also occur in the internal portion of the primary cortex. In *Thunbergia* the innermost layer of the primary cortex is formed by an endodermis, and adjoining this internally is a pericycle, with or without groups of bast-fibres. In *Mendoncia* there is a composite and continuous sclerenchymatous ring in the pericycle.

A rather large number of cases of **anomalous structure** in the stems have already been discovered in this Order, some of them being in lianes, whilst others occur in species which are not lianes.

Firstly, medullary bundles have been observed in species of *Acanthus* (*A. longifolius*, *A. mollis* and *A. spinosus*) by Vesque, Hérail and J. E. Weiss; these bundles as a rule form four groups, and are collateral with inverse orientation of wood and bast; sometimes, however, they show transitions to concentric structure, owing to the enclosure of the phloem by the xylem. According to J. E. Weiss they have the same course as the medullary bundles of *Campsis radicans* (Bignoniaceae, q.v.). Similar medullary bundles are met with in other cases (*Pseudocalyx*, *Mendoncia*, *Thunbergia* pro parte), but these genera are also characterized by further anomalies in their stems, as will be described later.

The Barlerieae and the genus *Nelsonia* are specially characterized by the possession of intraxylary phloem. Since Vesque first mentioned the occurrence of soft bast in the medullary sheath in *Barleria*, I have been able to demonstrate it in twenty-seven species of this genus (enumerated in my 'Holzstruktur'), and in *Barleriola solanifolia*, Oerst., *Lepidagathis cuspidata*, Nees, *L. prostrata*, Dalz., *L. terminalis*, Hochst., *Neuracanthus sphaerostachyus*, Dalz. and *Lophostachys montana*, Mart., and recently I have found it in *Somalia diffusa*, Oliv. According to Lindau, intraxylary phloem occurs in all the genera of the Barlerieae, with the exception of *Crabbea* and *Periblema*, in which I had already demonstrated the absence of this feature, as stated in my 'Holzstruktur'; thus, in addition to the genera cited above, intraxylary phloem is present in the two monotypic genera *Glossochilus* and *Volkensiophyton*, as one must assume from Lindau's description. At present I am unable to accept Lindau's statement that intraxylary phloem is wanting in a few species of *Barleria*, the names of which he does not give. I have already pointed out in my 'Holzstruktur' that the differentiation of the intraxylary soft bast varies in the genus *Barleria*, and is sometimes of such a kind that the presence of this tissue may be easily overlooked. Usually the intraxylary soft bast is only developed in the form of small groups of cells at the margin of the pith, frequently also it penetrates into the xylem-ring, and the number of phloem-bundles is often small, e.g. in *B. coerulea*, Roxb. In the genus *Nelsonia* intraxylary phloem has been shown to occur in *N. canescens*, Nees and *N. tomentosa*, Willd. (Tchouproff).

Interxylary as well as intraxylary phloem occurs in the genera of the Barlerieae mentioned above (*Barleria* incl. *Somalia, Barleriola, Lepidagathis, Lophostachys* and *Neuracanthus*, and, according to Lindau, probably *Glossochilus* and *Volkensiophyton* also). In most cases the interxylary phloem consists of small islands of soft bast, but in *Lophostachys montana*, Mart. it is composed of rather large groups, which are arranged concentrically at some distance from the pith. As a rule the islands of soft bast, which in *Barleria*, according to Chodat's investigations are given off internally by the cambium, are present in large numbers; when this is the case, they are to be found in quite young branches, as in twenty-six of the species of *Barleria* which I examined. Sometimes, however (e.g. in *Barleria flava*, Jacq.), the interxylary soft bast develops at a relatively late stage, and is not found in branches of less than 8 mm. diameter. Consequently, until further investigations have been undertaken I cannot accept Lindau's statement that interxylary phloem is wanting in certain species of *Barleria* (the names of which are again not given), although such exceptional cases are possible[1]. Interxylary islands of soft bast are also found in other members of the Order, namely in the species of *Thunbergia*, belonging to the section *Hexacentris*, and in certain other representatives of the Thunbergieae; in the latter case they accompany bast-wedges, and from these some of the islands arise. This leads us to consider the anomalous structure of the stem in the species of *Thunbergia*; after preliminary observations had been made by Vesque and Radlkofer, this subject has recently been thoroughly investigated by Roulet.

In the species of *Thunbergia*, belonging to the section *Hexacentris* (*T. coccinea*, Nees, *T. laurifolia*, Lindl., *T. mysorensis*, T. Anders., *T. Harrisii*, Hook., *T. parva*, Roulet, *T.* '*sinuata*, Wall.' and *T. grandiflora*, Roxb.), the wood contains typical islands of soft bast in the form of bands, which alternate with corresponding bands of wood on the same radii (Fig. 147). These bands only arise in the interfascicular tissue of the xylem-ring, and at first they only appear on two opposite sides of the transverse section of the stem, corresponding to the position of the furrows. At the points at which the anomaly appears the growth in thickness of the vascular ring is considerably increased. Subsequently, however, the anomaly extends to the entire transverse section of the branch, band-shaped islands of soft bast being formed on all sides. According to the investigations of Radlkofer, Chodat and Roulet, but contrary to those of Hérail, the islands of soft bast are developed from the inner side of the cambium. The anomalous structure, found in the branches of certain other Thunbergieae, appears at first sight to be essentially different from the anomaly just described in *Thunbergia coccinea*, &c., but on closer examination one finds that fundamentally it approaches the latter type. We will first consider *T. alata*, Boj. and *T. reticulata*, Hochst.; in both these species a transverse section of the young branch shows wedges of soft bast on the sides, on which the furrows occur; these wedges are given off internally by the cambium, like the islands of soft bast in *Hexacentris*. They grow in thickness owing to the activity of the cambium, and become narrower externally in consequence of an increase of wood at their margins; finally they become embedded in the tissue of the wood. In this way interxylary islands of soft bast appear in the thicker branches; they are distinguished from those of the species of *Hexacentris* by their irregular shape, and also by the fact that the sieve-tubes are not uniformly distributed within them, but are restricted to those parts which have xylem immediately contiguous to them externally. In the structure of its stem *Thunbergia fragrans*, Roxb. does not differ very

[1] O. Tchouproff examined five other species of *Barleria* (not examined by me) and found both intraxylary and interxylary phloem in them.

widely from the type just described; there are wedges of soft bast having the same mode of origin as in *T. alata*, and additional small islands of soft bast in the wood. The same structure as occurs in *T. fragrans* is also found in *T. tomentosa*, Nees, *T. lutea*, T. Anders., *T. convolvulifolia*, Baker, *T. chrysops*, Hook., *T. hastata*, Dcne., *T. angulata*, Hils. et Boj. and *T. Stuhlmanniana*, Lindau. In another group of species (viz. *T. atriplicifolia*, E. Mey., *T. capensis*, Thunb., *T. cyanea*, Boj., *T. hispida*, Lindau, *T. hirta*, Sond., *T. cerinthoides*, Radlk., *T. gentianoides*, Radlk., *T. lancifolia*, Moore, *T. angolensis*, Moore, *T. hyalina*, Moore, and *T. Cycnium*, Moore) the structure of the branch

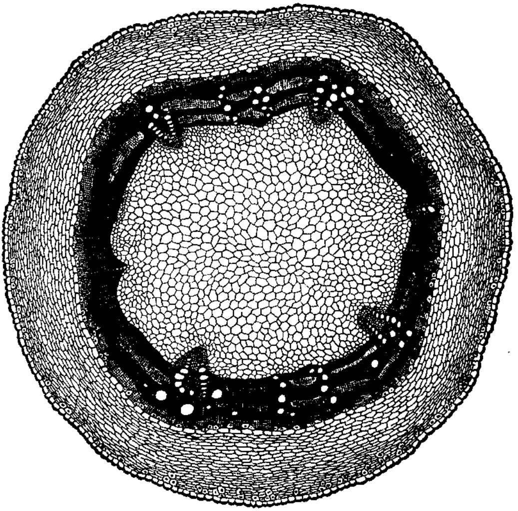


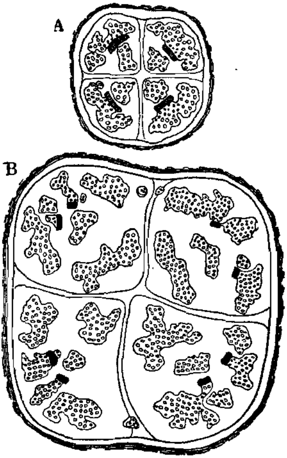
FIG. 147. Diagrammatic transverse section of a branch of *Thunbergia coccinea*, Wall., showing the peculiar distribution of the interxylary islands of soft bast, the peculiar differentiation of the xylem-ring and the subepidermal groups of sclerenchymatous fibres. The small acicular crystals of oxalate of lime, which are present in abundance in the pith, are omitted.—Original.

differs essentially from that of the species previously mentioned, since islands of soft bast do not occur in the wood. According to Roulet a certain number of these species (viz. *T. atriplicifolia*, *T. capensis*, *T. cyanea*, *T. hispida* and *T. hirta*) agree, to some extent, with the species previously referred to, for they possess wedges of bast on the sides of the stem on which the furrows occur, and these wedges are partly formed by tissue produced from the inner side of the cambium (like the interxylary phloem of *Hexacentris*), and partly by tissue given off externally by the cambium (like normal soft bast). The other species (viz. *T. Cycnium*, *T. angolensis*, *T. hyalina*, and *T. gentianoides* [1]),

[1] Roulet makes no statements regarding the structure of *T. lancifolia* and *T. cerinthoides* (see above).

as well as ***Meyenia Hawtayniana***, Nees, exhibit a somewhat different type of structure. Like the others they also have bast-wedges, but these consist entirely of soft bast-tissue, given off externally by the cambium, while thin-walled tissue, devoid of sieve-tubes, is produced on the inner side of the cambium. Special anomalies in the structure of the stem have been described by Roulet in ***Thunbergia annua***, Hochst., *T. **Fischeri***, Engl., *T. **longifolia***, Lindau, *T. **armipotens***, Moore, *T. **huillensis***, Moore and *T. **rufescens***, Lindau,* and these will be briefly referred to in the order in which the species have been enumerated. On the other hand, the branches of *T. **adenocalyx***, Radlk., *T. Holstii*, Lindau, *T. Vogeliana*, Benth., *T. **Kamerunensis***, Lindau, *T. **affinis***, Moore and *T. **erecta***, Anders. have normal structure. A transverse section of a branch of *T. **annua***, Hochst. shows a xylem-ring uniformly developed, and containing a few relatively large islands of soft bast in the neighbourhood of the pith. *T. Fischeri*, Engl., besides possessing wedges of soft bast, like those of *T. Cycnium*, has interxylary islands of soft bast at two opposite points in the interfascicular tissue; these islands of bast are situated very near the pith, and are in part united with it; their mode of development is unknown, but is probably the same as in *T. coccinea*, &c. In *T. **longifolia***, Lindau, masses of tissue with thin walls and devoid of sieve-tubes are found at the margin of the pith, and form wedges which penetrate into the wood. Far more complicated anomalies in the stem-structure have been observed in *T. **armipotens*** and *T. **huillensis***, and are probably characteristic of *T. **rufescens*** also, but older branches of this species have not yet been examined. In the first two species a transverse section through a young branch shows a well-developed wedge of bast on both the furrowed sides of the stem, and four portions of the xylem-ring, which contain numerous vessels, correspond in position to the four angles of the stem, and are separated from one another by interfascicular tissue. At a somewhat later stage four medullary groups of wood and bast are developed at the margin of the pith opposite these four portions of the xylem-ring. Finally fission of the xylem-ring takes place, separating it into four masses, which correspond to the four portions, provided with abundant vessels; the four masses of wood then become surrounded by cambial tissue. Sometimes smaller bundles of wood arising from the interfascicular tissue appear between the four principal masses. Essentially the same anomaly in the structure of the branch as occurs in *T. **armipotens*** and *T. **huillensis*** is found in ***Mendoncia*** sp., Regnell n. III, 949 a, according to Radlkofer, in ***Mendoncia Velloziana***, Mart., according to H. Schenck (Fig. 148), and in ***M. Schomburgkiana***, Nees, according to Tchouproff. A similar fission of the mass of the wood into four portions has been demonstrated

A



B

Fig. 148. Fission of the xylem-mass in *Mendoncia Velloziana*, Mart.: *A*, Young stem, × 6; *B*, Older stem, × 3.—After H. Schenck.

by Gilg in his newly-established genus *Afromendoncia* (with two species), and especially in *A. phytocrenoides*; the fission originates in wedges of soft bast, which are present from the first. Medullary xylem-groups, like those of *Mendoncia* or *Thunbergia armipotens*, have not been observed in this genus, but masses of stone-cells are present, shutting in the wedges of soft bast (to which the fission is due) from the pith and the cortex, and thus preventing any compression of the soft bast in case of torsions occurring in the stem. Fission of the original mass of wood probably also occurs in later stages in the monotypic genus *Pseudocalyx* (with *P. saccatus*, Radlk.), but only relatively young branches have been examined. Radlkofer demonstrated the occurrence of four wedges of soft bast, placed cross-wise, in the xylem-mass of *Pseudocalyx*, and also the commencement of a new inversely orientated ring of wood and bast at the margin of the pith [1].

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MYOPORINEAE.

The most important anatomical character of the Order (especially as compared with the allied Selagineae) is constituted by the schizogenous secretory cavities occurring in all the Myoporineae, with the exception of the genera *Oftia* and *Zombiana*, and not infrequently giving rise to transparent dots in the leaves. Additional characteristic features are found in the glandular hairs, in which the head is, in almost all cases, divided by vertical walls only (though in rare cases it is unicellular), whilst in the structure of the axis, the simple perforations in the vessels, the wood-prosenchyma with simple pits, and the superficial formation

[1] Sometimes the root of the Acanthaceae shows anomalies similar to those of the branch. Thus according to Roulet the interxylary bands of soft bast also appear in the root in *Hexacentris coccinea*; similarly small islands of soft bast are found in the wood of the root in *T. alata* and *T. reticulata*, but are wanting in *T. annua*. Further, according to H. Schenck, cleavage of the xylem-ring and secondary formation of masses of wood and bast in the pith occurs in the root of *Mendoncia Velloziana*. I may add that in the genus *Thunbergia* interxylary phloem is sometimes met with in the petiole (e.g. in *T. grandiflora*).

of periderm are characteristic. The genus *Oftia* alone possesses intraxylary phloem (Briquet). The stomata are surrounded by three or more epidermal cells. Oxalate of lime is excreted chiefly in the form of small clustered or acicular crystals, rarely (in sclerenchymatous cells) in the form of larger solitary crystals. The occurrence of inulin accompanying starch in the branch and root of *Myoporum* is also noteworthy. In addition to the glandular hairs already mentioned, simple, uniseriate, and (in *Eremophila*) multicellular, branched trichomes take part in the formation of the hairy covering.

The occurrence of **secretory cavities** is almost universal, according to existing investigations (viz. those of Bokorny and Briquet), which deal with all the genera. The cavities are wanting in the genus *Oftia*, which also differs from the other members of the Order in possessing intraxylary phloem; on account of its exomorphic characters, however, it is retained amongst the Myoporineae, although it constitutes a separate tribe (the Oftieae); the cavities are also absent in *Zombiana*, but in none of the other genera; further details regarding *Zombiana* will be given in an appendix to the Order. Bokorny's statement regarding the absence of secretory cavities in *Eremophila longifolia*, F.v. Müll. and *Pentacoelium bontioides*, S. et Z. (= *Myoporum bontioides*, A. Gray) is incorrect, and we may add that these cavities are present in the leaf of *Myoporum bontioides*, and, at any rate, in the cortex of the branch in *Eremophila longifolia*. In *Eremophila Oldfieldii*, F. v. Müll., I have likewise only been able to find the secretory cavities in the branch and not in the leaf. In other cases (e.g. in *Myoporum acuminatum*, R. Br. and *Bontia daphnoides*, L.) the secretory cavities are developed in both leaf and stem. In the leaf they are not confined to any special region of the mesophyll. They are often of considerable size, and frequently give rise to pellucid dots; in some cases they may even cause raised dots, as in *Myoporum parvifolium*, R. Br. and *M. tuberculatum*, R. Br. In the axis they are confined to the pith and primary cortex. Contrary to Van Tieghem's results, Briquet met with secretory cavities in the root also, viz. in the phelloderm of the older roots of *M. acuminatum*, R. Br. The secretion formed in these cavities is of various kinds, but probably always consists of an oily resinous substance. According to Van Tieghem, Leblois and Briquet, the development of the secretory receptacles is schizogenous, and not lysigenous, as was assumed by Martinet, De Bary, Höhnel and Bokorny. The presence of a distinct, and for the most part many-layered epithelium lining the secretory cavities, also suggests the former mode of development; sometimes the innermost layer of the epithelium becomes subsequently absorbed, the gland thus becoming schizolysigenous (Briquet).

The **structure of the leaf** has been examined in detail by Briquet and also by myself in the following species: *Myoporum bontioides*, A. Gray, *M. acuminatum*, R. Br.; *Eremophila Brownii*, F. v. Müll., *E. longifolia*, F. v. Müll., *E. Macdonellii*, F. v. Müll., *E. Oldfieldii*, F. v. Müll., *E. Latrobei*, F. v. Müll.; *Bontia daphnoides*, L. The **mesophyll** exhibits centric structure in almost all cases where this character can be ascertained with sufficient certainty in herbarium-material, as in *E. Macdonellii* and *E. Oldfieldii*. Bifacial structure has only been shown to occur in the two species of *Oftia*. The **stomata** are usually found on both sides of the leaf; they are restricted to the lower side in *Oftia* only. They are in most cases accompanied by three subsidiary cells (e.g. in *Myoporum acuminatum*, *Bontia daphnoides* and *Eremophila Brownii*); in other species (e.g. *E. Latrobei*) this is not the only type present, some of the stomata being surrounded by a larger number of epidermal cells; the latter type is quite general in *Eremophila Oldfieldii* and also in *Oftia*. The guard-cells either lie on a level with the epidermis or project above it. According to Briquet, the **epidermal cells** of the leaf frequently project as papillae, and show considerable variations as

regards the thickness and cuticularization of the outer wall in the individual species. The structure of the **veins** of the leaf can also be employed in specific diagnosis. In many members of the Order the principal vein is embedded in the assimilatory tissue of the leaf; in other cases a special collenchymatous tissue surrounds the system of vascular bundles in the vein. Sclerenchyma accompanying the vascular bundles has only been found in *Oftia* (by Briquet), but collenchymatous tissue is frequently present in its place.

The **hairy covering** consists of clothing and glandular hairs. The clothing hairs are either simple, uniseriate trichomes (e.g. in *Eremophila longifolia* and in *Oftia*), or branched, multicellular hairs (e.g. in certain species of *Eremophila*). The water-storing trichomes of *Eremophila alternifolia*, R. Br., figured by Briquet (Fig. 26), arise from nearly all the epidermal cells of the leaf, and constitute a special form among the simple hairs. According to my own investigation (though not quite in agreement with Briquet's Figure 18), the branched hairs of *E. Brownii* consist of a row of short cells, which are protruded laterally in various directions like hairs; the whole trichome thus comes to have the appearance of a stellate hair when viewed from above; in other species, such as *E. Latrobei*, this 'sympodial' type is less distinct, since some of the cells constituting the branches do not take part in the formation of the main axis of the trichome. My investigation showed that the glandular hairs possess varied structure in the individual species, but agree in the fact that the glandular head is in almost all cases[1] divided by vertical walls only.

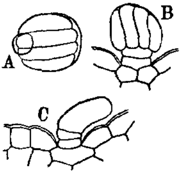

FIG. 149. Glandular hairs of *Myoporum acuminatum*, R. Br.: A, Surface-view; B and C, Appearance in transverse section.—Original.

Eremophila Brownii has glandular hairs with a short, unicellular stalk and a disc-shaped head, which is either divided by four vertical walls, forming an orthogonal cross, or by a larger number of vertical walls arranged approximately in a radial direction[2]; in the latter case each of the glandular cells of the head commonly contains a small clustered crystal. In *E. Latrobei* the leaf bears external glands, which have a somewhat longer stalk composed of two cells, and a small head with a single vertical division-wall; occasionally glandular heads of this kind also terminate the branches of the branched hairs occurring in this species. The external glands of *E. Macdonellii* have a still longer stalk consisting of a row of four cells, of which the uppermost is differentiated as a kind of neck-cell; the disc-shaped head is divided by a relatively large number of radially placed vertical walls into a number of cells, each of which encloses a clustered crystal. *Bontia daphnoides* has glandular hairs with a short stalk and a head which is divided into a large number of cells by vertical walls showing varied orientation. The external glands found in *Myoporum acuminatum* (Fig. 149) and *M. bontioides* are of a very curious type. They have a short stalk, which is composed of either one or two cells, and on this the approximately disc-shaped head is seated in an eccentric and oblique position; the head is divided by a few vertical walls arranged parallel to one another. Finally, in the genus *Oftia*, examined by Briquet, the glandular hairs have a uniseriate stalk, with cells becoming shorter towards the apex, and a head which is either unicellular or divided by vertical walls.

Oxalate of lime, both in the leaf and axis, is usually excreted in the form of small clustered crystals. The latter sometimes occupy the cells of the mesophyll in special abundance (e.g. in *Eremophila longifolia* and *E. Oldfieldii*); in *Bontia*, clustered crystals, besides occurring in the mesophyll, are

[1] According to Briquet abundant horizontal divisions also occur in the head in *E. maculata*, F. v. Müll., but I only found this to be the case exceptionally in the glandular hairs on the leaf-base.

[2] Briquet's statement, that the glandular heads are unicellular in *E. Brownii*, is incorrect.

also present in the epidermis, accompanying rod-like crystals. In the mesophyll of *Eremophila Drummondii*, F. v. Müll., small acicular crystals are just as abundant as the clustered crystals in the case of *E. longifolia*. In the stem clustered crystals have been observed in the pith and primary cortex. In *Eremophila Oldfieldii* rather large solitary crystals are found in the sclerenchymatous parenchyma-cells of the pericycle; they are also met with in the pith of the same plant, where they have rounded facets. Here we may refer to the occurrence of special, doubly refractive, crystalline bodies in the pith of species of *Myoporum* (*M. ellipticum*, according to Van Tieghem, *M. laetum*, Forst. and *M. serratum*, R. Br., according to Briquet); these structures are disc-shaped, and include a central body like a clustered crystal; they are soluble in hot water and dilute acids. Van Tieghem, as mentioned above, found considerable quantities of **inulin** in *Myoporum* in the bast-parenchyma of the stem, and in the cortex of the root. In addition to this, starch occurs in the stem of *Myoporum*.

In the structure of the **axis** we may specially point out that, according to Briquet, **intraxylary phloem** is developed in *Oftia* only, and occurs in the form of small groups at the margin of the pith, a certain number of them being situated at some distance from the ring of vascular bundles. This intraxylary phloem is only developed at a relatively late stage.

In a transverse section of a branch, the mass of **wood** in the Myoporineae (incl. *Oftia*) shows narrow, uniseriate or biseriate medullary rays, and small vessels (maximum diameter = ·03–·04 mm.), which mostly exhibit radial arrangement. The perforations of the vessels are simple; the vessel-wall bears bordered pits in contact with parenchyma. Only in *Myoporum salsoloides*, Turcz. has spiral thickening of the pitted vessels and tracheids been observed (Briquet). The wood-parenchyma is scantily developed, and the wood-prosenchyma bears simple pits. The most important points to be mentioned in the structure of the **cortex** are the subepidermal[1] formation of periderm (*Oftia* included), and the presence of groups of sclerenchyma, or of a more or less closed sclerenchymatous ring in the pericycle. The sclerenchyma of the pericycle consists of small isolated groups of fibres (e.g. in *Bontia daphnoides*), or of a loose ring of fibres and stone cells as in *Myoporum acuminatum*. It remains to mention (1) the weakly developed decurrent foliar wings ('macroptères' of Briquet) found on the stem in the species of *Oftia*, the stomata on the stem being confined to these wings, and (2) the wide air-spaces, which have been observed in the primary cortical parenchyma of *Myoporum chinense*, Gray, *M. laetum*, Forst., *M. platycarpum*, R. Br. and *M. salsoloides*, Turcz.

Appendix: On the genus *Zombiana*.

Briquet doubts the correctness of the view that this monotypic genus, established by Baillon, belongs to the Myoporineae.

The most noteworthy anatomical feature is the absence of secretory cavities in *Z. africana*, Baill. The leaf has centric structure. Both surfaces bear stomata, which are mostly surrounded by four epidermal cells. The epidermal cells of the leaf have a polygonal outline, and are papillose. The petiole contains three vascular bundles; of these the median bundle is large, and the lateral bundles are rounded in section. Regarding the structure of the branch, we may note that the periderm arises subepidermally, that the pericycle contains isolated groups of bast-fibres, and that the wood is composed of uniseriate medullary rays, wood-prosenchyma bearing simple pits and sometimes septate, vessels and tracheids. Oxalate of lime has been observed in the middle layer of the leaf in the form of clustered crystals. The hairy covering consists of simple, uniseriate trichomes.

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[1] In the root of *Myoporum* the development of cork takes place in the pericycle (Briquet). Regarding the formation of the metaxylem (of Van Tieghem) in the root of *Myoporum*, see Briquet, loc. cit.

Literature: Martinet, in Ann. sc. nat., sér. 5, t. xiv, 1871, p. 199 et seq.—De Bary, Vergl. Anat., 1877.—Höhnel, Sekretionsorg., Sitz.-Ber. Wiener Akad., Bd. lxxxiv, Abt. 1, 1881, p. 578.—Szyszylowicz, Sekretbeh. (Polish), Pamietnik Akademii Umijetnosci W. Krakowie, t. vi, 1881, p. 23 et seq. and Tab. vii.—Bokorny, Durchs. P., Flora 1882, p. 372 et seq. and sep. copy, pp. 26–7.—Van Tieghem, Canaux sécrét., Ann. sc. nat., sér. 7, t. i, 1885, pp. 55–7.—Solereder, Holzstr., 1885, pp. 202–3.—Leblois, in Ann. sc. nat., sér. 7, t. vi, 1887, pp. 256–8 and pl. 8.—Wettstein, in Natürl. Pflanzenfam., IV. Teil, Abt. 3 b, 1895, pp. 355–6.—Briquet, *Zombiana*, Bull. de l'Herbier Boissier, t. iv, 1896, pp. 324–7; Mélanges, Bull. Laborat. de bot. gén. de l'université de Genève, vol. i, n. 1, 1896, p. 7 and Appareil végétatif des Phrymacées etc., Mém. Soc. phys. et hist. nat. de Genève, t. xxxii, 2e partie, n. 8, 1896, sep. copy, pp. 80–154.

SELAGINEAE.

The most characteristic anatomical feature in this Order is constituted by small glandular hairs (Fig. 150), consisting of a basal cell belonging to the epidermis, a short stalk-cell, and a head, which is composed of two cells separated by a vertical wall, or more rarely of four cells, owing to the presence of two vertical walls, arranged in the form of a right-angled cross; these glands either occur on the surface of the organs or are depressed, and in the latter case they sometimes secrete lime. Internal secretory organs are not present, and this is a point of difference from the allied Myoporineae. The stomatal apparatus does not conform to any definite uniform type. Oxalate of lime, in the rare cases in which it occurs, is excreted in the form of small prismatic or rod-shaped crystals. In all the investigated genera (*Hebenstreitia, Dischisma, Selago, Microdon, Agathelpis, Globularia*) the wood has narrow medullary rays, simple perforations in the vessels, and bordered pits on the vessel-walls in contact with parenchyma; the wood-prosenchyma bears bordered pits in *Globularia* only; elsewhere it has simple pits. Isolated bundles of sclerenchyma may or may not be present in the pericycle. The development of cork may be either superficial or internal[1].

The following points may be mentioned regarding the structure of the leaf. The structure varies even within the limits of the genus *Globularia*; thus *G. stygia* has a mesophyll with bifacial structure; in *G. ilicifolia* the mesophyll is centric and composed of palisade-tissue, whilst in *G. trichosantha* it is centric, and consists of approximately isodiametric cells. The stomata occur on both sides of the leaf in all the investigated species. Usually each pair of guard-cells is surrounded by several ordinary epidermal cells, but the same leaf-surface sometimes bears stomata which follow the Rubiaceous or Caryophylleous types, besides those of the type just mentioned. In many species of *Globularia* the epidermal cells both of the leaf and stem contain chlorophyll, either permanently or temporarily. Branched sclerenchymatous cells have only been met with in the mesophyll of *Globularia orientalis*. According to Heckel, the structure of the principal veins is of systematic value in the diagnosis of species of *Globularia*. In *G. Alypum*, *G. arabica*, *G. cordifolia* and *G. nudicaulis*, the principal veins are embedded; their fibrovascular system is surrounded on all sides by chlorophyll-bearing tissue, and contains a firmly constructed xylem. In the remaining species of *Globularia*, on the other hand, the principal veins are vertically transcurrent, since collenchyma extends from the fibro-vascular system (which here has a lax xylem) to the epidermis; the collenchyma is either present on both sides (*G. stygia*) or is confined to the upper (*G. incanescens*) or lower side

[1] The preceding summary and the following statements are mainly based on Heckel's work and on my own casual investigations. Heckel's investigations extend to the following species: *Globularia Alypum*, L., *G. arabica*, Jaub. et Spach, *G. cordifolia*, L. with var., *G. ilicifolia*, Willk., *G. incanescens*, Viv., *G. nudicaulis*, L., *G. orientalis*, L., *G. salicina*, Lam., *G. stygia*, Orph., *G. tenella*, Lange, *G. trichosantha*, Fisch. et Mey., *G. vulgaris*, L., *G. Willkommii*, Nym., *Hebenstreitia dentata*, L., *H. integrifolia*, L., *H. tenuifolia*, Schrad., *Selago corymbosa*, L., *S. spuria*, L., *Gymnandra armena*, Boiss.; I examined the following species: *Hebenstreitia cordata*, L., *H. dentata*, L., *Dischisma hispidum*, Choisy, *Selago corymbosa*, L. and *Agathelpis angustifolia*, Choisy.

(*G. orientalis*). Regarding the mechanical system of the median veins, we may add that in *Globularia* sclerenchyma may be present accompanying the vascular bundles in varied abundance.

Oxalate of lime has been observed, in the form described above, in the epidermis of the leaf and branch in *Globularia Alypum* and *G. arabica*; each epidermal cell contains a single crystal or an aggregate of a few crystals. Oxalate of lime appears to occur in much greater abundance in the floral organs, but there also it is only found in the epidermis. In the cortical tissue it has only been met with in *Hebenstreitia tenuifolia*, Schrad. (Kupffender). The small crystals which occur in the epidermis in *Globularia cordifolia* do not consist of oxalate of lime.

The **glandular hairs**, the nature of which has been described above, are present in all the genera and species investigated. The head usually consists of two cells, and generally has two knobs, owing to the arched form of the cells ('glandes bicipités' of Heckel); it is rarely spherical (*Microdon cylindricus*). Heads, composed of four cells, are common in *Globularia nudicaulis*, but according to Kupffender they are also present in *G. vulgaris*. The secretion of lime by the glands has been demonstrated by Heckel in *Globularia Alypum*, *G. arabica*,

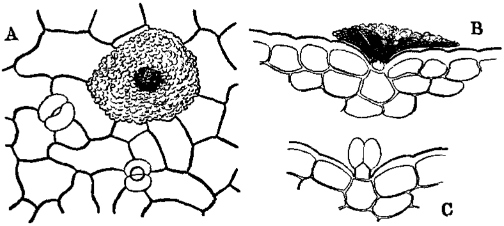

FIG. 150. Chalk-glands of *Selago spuria*, L.: A, Superficial section of the leaf with one external gland, covered by a scale of lime, and another decalcified; B, Gland with calcareous scale in section; C, Gland in section after the solution of the scale.—Original.

G. ilicifolia, *G. incanescens*, *G. orientalis*, *G. vulgaris*, *Hebenstreitia dentata*, *H. integrifolia*, *Dischisma tenuifolia*, *Selago corymbosa* and *S. spuria*; the lime forms definite scales, which fill the small pits situated above the glands, their margins resting on the surface of the organ. Side by side with the glandular trichomes, simple uniseriate clothing hairs, composed of a small number of cells, are found in most members of the Order. The somewhat abundant hairy covering on the bracts and sepals of *Globularia* apparently consists of uniseriate clothing hairs, but these hairs are derived from glandular trichomes with long stalks, the glandular head, which is composed of one, two or four cells, having fallen off.

To the previous statements regarding the structure of the **wood**, we may add that the vessels have relatively small lumina (maximum diameter = ·024–·05 mm.); the cells of the uniseriate or biseriate medullary rays are sometimes more prosenchymatous than parenchymatous in shape when seen in tangential section; the wood-parenchyma is scantily developed; in *Selago corymbosa* spiral thickening of the vessel-wall occurs.

The development of cork takes place subepidermally in *Hebenstreitia dentata*, but is internal to the pericyclic sclerenchyma in *Selago corymbosa*. The outer portion of the primary **cortex** is sometimes collenchymatous. In the majority of the species of *Globularia*, in *Hebenstreitia cordata*, *H. dentata*,

Dischisma hispidum and *Selago corymbosa*, the pericycle contains isolated sclerenchymatous groups, which may consist either of parenchymatous (*Dischisma hispidum*) or fibrous cells (*Selago corymbosa*).

Literature: Solereder, Holzstr., 1885, p. 203.—Heckel, Écailles et glandes calc. des Globul. et des S., Compt. rend., t. cix, 1889, pp. 35–8.—Solereder, *Melananthus*, Sitz.-Ber. deutsch. bot. Gesellsch., 1891, Gen.-Vers.-Heft, pp. 72, 73.—Heckel, Schlagdenhauffen and Mourson, Ét. monogr. des Glob. etc., Bull. Soc. scient. Flammarion, 1888–90, Paris, 1890.—Kupffender, Anat. d. Globular. u. S., Diss., Erlangen, 1891, 60 pp.—Wettstein, in Natürl. Pflanzenfam., IV. Teil, Abt. 3 b, 1895, pp. 270–1.

VERBENACEAE.

1. Review of the Anatomical Features. The most characteristic features are as follows: the wood-prosenchyma bears simple pits, and is sometimes septate; in the vessels simple perforations predominate, while scalariform perforations are rarely found accompanying them; glandular hairs occur, the head being unicellular, or divided by vertical walls. Apart from glandular hairs, the hairy covering (Fig. 151) is constituted by the following types: ordinary unicellular or uniseriate trichomes (the latter sometimes with elongated terminal cells); reduced, silicified, unicellular hairs (*Petraea*); unicellular, two-armed hairs (*Lippia*); unicellular cystolith-hairs, accompanied by cystolith-like structures in the subsidiary cells; bracket-hairs (*Priva*); variously branched, multicellular trichomes (many Chloantheae and *Tectona*); and peltate hairs with a characteristic structure (*Clerodendron, Chloanthes, Pityrodia*). As a rule the stomata are surrounded by a considerable number of ordinary epidermal cells, but the Caryophylleous type, with subsidiary cells placed transversely to the pore, also occurs. The development of cork may take place superficially or in the neighbourhood of the pericycle. Internal secretory organs are not present. The nectarial glands found on the lower side of the leaf in species of *Clerodendron*, &c., belong to the category of external glands. Oxalate of lime is excreted in the form of small acicular or prismatic crystals. The following anomalies in the structure of the axis are met with: (*a*) the formation of furrows and wings on the surface of the stem in *Lantana*, sometimes leading to a subsequent splitting of the stem into four longitudinal portions; and (*b*) in *Avicennia*, successive rings of growth of extrafascicular origin.

2. Structure of the Leaf. The anatomy of the leaf has been examined by Vesque in a general comparative manner, and by Briquet in greater detail in certain genera belonging to the tribes Phrymeae, Stilbeae and Chloantheae [1]. The mesophyll may be bifacial or centric in structure. The **stomata** either occur on both sides of the leaf, or only on the lower side; when an abundant hairy covering is present, they are sometimes strongly prominent; they are surrounded by three [2], four, or more epidermal cells. In *Stachytarpheta volubilis*, according to Vesque, stomata of the type just mentioned are accompanied by others, which have two subsidiary cells placed transversely to the pore; stomata of the latter type only are found in *Clerodendron sansibarense*, Gürke, *Lippia nodiflora*, Michx. and *Petraea volubilis*, L. (Fig. 151, *A*). The **epidermal cells** on the outer side of the rolled leaves occurring in certain members

[1] Vesque examined species of *Aegiphila, Callicarpa, Citharexylum, Clerodendron, Duranta, Petraea, Premna, Stachytarpheta, Verbena* and *Vitex*; Briquet investigated species of *Phryma* (Tribe Phrymeae), of *Campylostachys, Stilbe, Euthystachys, Eurylobium* and *Xeroplana* (Tribe Stilbeae) and of *Lachnostachys, Dicrastyles, Chloanthes, Pityrodia, Cyanostegia* and *Spartothamnella* (Tribe Chloantheae). Regarding the structure of the peculiar leaves of *Acantholippia riojana*, Hier. see Goebel, 1891, loc. cit.

[2] In *Citharexylum quadrangulare* the development of the stomatal apparatus follows the Cruciferous type (Vesque).

of the Order (species of the genera of Stilbeae examined by Briquet, and also of *Chloanthes, Dicrastyles, Lachnostachys* and *Pityrodia*) generally have large lumina. Gelatinization of the epidermis of the leaf has not been observed; on the other hand a hypoderm of several layers is found on the upper side of the leaf in the species of *Avicennia* (Wille, Schimper). The leaf-teeth of *Phryma* contain the termination of a vascular bundle provided with an epithema, and have a group of water-pores in the epidermis above.

The fibrovascular system of the **petiole** has a varied structure. In most cases it forms a ring or an arc, with one or two pairs of additional vascular bundles on its upper side. In *Premna scandens* the vascular bundles are arranged in a scalariform manner; in *Lippia citriodora* and *Vitex agnus castus* there are a number of groups of bast-tissue on the inner side of the fibrovascular arc. For details see Vesque, Petit and Briquet, ll. cc

Internal glands do not occur in the Verbenaceae. **Oxalate of lime**, in the form of small acicular or prismatic crystals sometimes having octahedral apices, or small spear-shaped crystals, is widely distributed[1] in the parenchymatous tissues of the leaf and axis (and also in the medullary rays of the wood). Aggregates, resembling clustered crystals (petiole of *Callicarpa americana* and *Vitex agnus castus*) and ordinary large solitary crystals (bast of *Tectona grandis*, L. f., and *Petraea arborea*, H. B. K.), are of rarer occurrence. Nuclear crystalloids have been met with in the leaf by Zimmermann in a plant cited as *Clerodendron Thompsoni* (probably = *C. Thomsonae*), and in *Verbena officinalis*.

The **hairy covering** is very varied, and will repay a detailed examination. Amongst the clothing hairs we may first refer to the simple, unicellular trichomes, of which the following are special forms: (*a*) the short conical hairs occurring on the leaf of *Vitex agnus castus*, and seated upon the vertical division-wall between two adjoining epidermal cells; (*b*) the short, strongly silicified trichomes of *Petraea volubilis*, L., which give rise to pointed conical irregularities on the leaf-surface, and are embedded singly in the thickened outer wall of the epidermal cells (Fig. 151, *A–B*); (*c*) the unicellular two-armed trichomes of *Lippia nodiflora*, Michx., the walls of which are strongly thickened and verrucose; and (*d*) the cystolith-hairs of *Verbena Caroliniana*, L., *Lippia Schaueriana*, Mart., *Lantana Sellowiana*, Lk. et Otto, and other species, in which the structure of the hairs is similar to that seen in the Boragineae, the base of the hair being surrounded by subsidiary cells containing cystoliths, as in that Order. We may mention here that the well-known silicified rosettes of cells on the leaf of *Tectona grandis* contain cystolith-like bodies, and that, generally speaking, calcification and silification frequently occur side by side; and lastly that cystoliths, independent of hairs, have not hitherto been observed in this Order, but may possibly occur. Simple uniseriate hairs are also widely distributed in the Verbenaceae (they are present, e.g., in *Callicarpa, Clerodendron* and *Vitex*, according to Vesque); in *Pityrodia salvifolia*, R. Br., they consist of either one or two short cells, and a long, terminal cell with thick walls; in the Stilbeae examined by Briquet, they are quite generally composed of a short thin-walled stalk-cell, seated on the epidermis, and a long terminal cell with thick walls. Other types of uniseriate hairs are: (*a*) the bracket-hairs of *Priva tuberosa*, Wats., which consist of an epidermal cell (serving as a basal cell to the hair), and a second cell, which is probably silicified and has its terminal portion bent like a hook, and thickened to such an extent that the lumen of the cell disappears at this point; (*b*) the small trichomes on the lower side of the leaves of *Avicennia nitida*, Jacq. (Fig. 151, *G*) and

[1] In species of *Aegiphila, Citharexylum, Clerodendron, Lantana, Premna, Stachytarpheta, Symphorema* and *Vitex*; see Möller, Vesque, Solereder, ll. cc.

A. officinalis, L.; excluding the epidermal cell which serves as a pedestal, these hairs consist of a short stalk-cell and a pear-shaped terminal cell, placed horizontally and excentrically on the stalk; these hairs give a dull appearance to the lower surface of the leaf in *A. nitida*, and a white appearance to that of *A. officinalis*. Very characteristic peltate hairs are found in the species of *Clerodendron* belonging to the group Squamata (see DC. Prodr. xi, 1847, p. 668 et seq.), and in certain species of *Pityrodia* and *Chloanthes*. In the peltate hairs of *Clerodendron squamatum*, Vahl. (Fig. 151, *C–D*) the variously shaped shield has an entire margin and consists of several layers of polygonal cells; it is seated on a plate of smaller area composed of a single layer of cells, and forming the stalk of the scaly hair; in the development of this lower

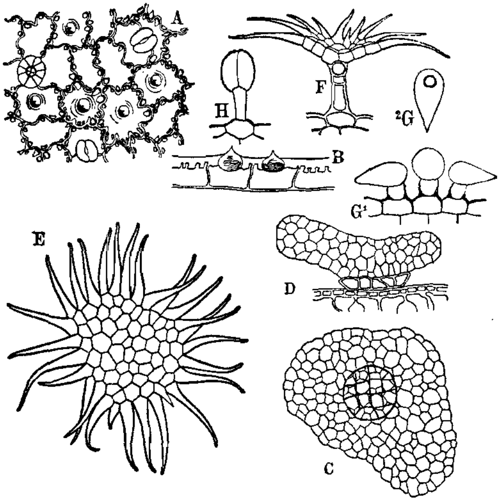

FIG. 151. A–B, *Petraea volubilis*, L.: A, Epidermis of the leaf in surface-view, B, in transverse section. C–D, Peltate hair of *Clerodendron squamatum*, Vahl. E–F, Peltate hair of *Pityrodia salvifolia*, R. Br. G, Trichomes on the surface of the leaf in *Avicennia nitida*, Jacq. H, Glandular hair of *Pityrodia salvifolia*.—C–D after O. Bachmann, the remainder original.

plate four cells are first formed by two vertical walls, crossing one another at right angles, and by further divisions, break up into 12–16 rather thick-walled cells (O. Bachmann). The small scales (lepides) of *Pityrodia* (Fig. 151, *E–F*) and *Chloanthes* agree in their structure; the stalk is uniseriate, often rather long, and composed of a few cells, which become shorter towards the shield; the latter consists of a layer of cells which are polygonal in surface-view, and are produced at the margin of the shield into very short (*Chloanthes loricata*, F. v. Müll.) or relatively long (*Pityrodia salvifolia*, R. Br.) rays. If we imagine the central polygonal cells of these peltate hairs reduced or absent we should obtain structures like stellate hairs, and these are present on the surface of

the leaf in *Pityrodia salvifolia*, where they accompany the scales, and have also been described in *P. atriplicina*, F. v. Müll. by O. Bachmann. In *P. Bartlingii*, Benth., we find different transitional forms between stellate hairs (like those described above) and variously branched trichomes, which have thi walls, but show no other points of agreement besides the uniseriate character of the main axis and the fact that the branches of the highest order consist of single, rather long cells. I have met with branched, usually thin-walled trichomes (which often appear like stellate hairs when examined with a lens), in *Lachnostachys Walcottii*, F. v. Müll., *Tectona grandis*, and *Chloanthes Stoechadis*, R. Br. (where they are almost dichotomously branched)[1]. Trichomes belonging to the same category are found in *Callicarpa americana*, L. (according to Vesque) and *Dicrastyles Stoechas*, Drumm. (according to Briquet); they have a structure approaching that of the well-known candelabra-hairs of *Verbascum*. Glandular hairs are widely distributed in the Order. The heads of these hairs are unicellular, bi- or multicellular, all the division-walls being vertical[2]. The glandular hairs may be classified under two categories, viz. (*a*) hairs with a relatively small head, which is either unicellular or divided by one or few vertical walls; and (*b*) hairs with a larger disc-shaped head composed of more numerous cells. The hairs of the first type have been observed in *Phryma*, in the Stilbeae examined by Briquet, in *Dicrastyles* and *Pityrodia*; they have a short, unicellular or multicellular stalk, which is sometimes elongated (occasionally composed of 5–8 cells in *Pityrodia*); the hairs of the second type always have short stalks. In the disc-shaped glandular hairs the structure is either the same as in the peltate glands of the Oleaceae (*Avicennia*, *Petraea*, Fig. 151, *A*), or the accumulation of secretion is subcuticular, as in the bladder-like integumental glands of the Labiatae (e.g. in *Pityrodia salvifolia*, R. Br.[3]). Sometimes the peltate glands in question are deeply sunk in the tissue of the leaf, and give rise to transparent dots[4] (*Callicarpa longifolia*, according to Bokorny, *Clerodendron aculeatum*, Griseb., according to Radlkofer). The description of the glandular hairs is naturally followed by that of the nectarial glands found on the lower side of the leaf in *Clerodendron fragrans*, and other species of the same genus; these have been examined by Reinke. A transverse section through one of these glandular dots shows that the epidermis here consists of cells elongated like a palisade; below the epidermis there is a layer of polygonal tabular cells, about sixteen times as large as the palisade-cells in surface-view, and having the walls perpendicular to the surface of the organ suberized; the secretion collects beneath the cuticle, and consists of a mixture of gum and sugar, the latter occasionally crystallizing out. The nectarial glands, mentioned by Delpino as occurring on the leaf-surface or petiole in species of *Callicarpa*, *Citharexylum* and *Duranta*, require further investigation.

3 Structure of the Axis. In the first place we may mention that, as stated by Briquet, the young branches of *Phryma* are quadrangular in section, whilst those of the Stilbeae and Chloantheae are generally polygonal (with three, four, or many sides). In some few Stilbeae and Chloantheae the stem is winged. Four strongly developed ' macroptera ' are found in certain species

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[1] Other examples of this type are the branched trichomes of species of *Cyanostegia* and *Spartothamnella* (according to Briquet), and probably also the stellate hairs of *Physopsis* and *Lachnocephalus*, mentioned by Briquet.

[2] According to Wille, however, colleters, with a unicellular stalk and a head consisting of two tiers of cells, occur on the rudimentary leaves in *Avicennia nitida*.

[3] Briquet also mentions disc-shaped glands as occurring in *Dicrastyles*, *Cyanostegia* and *Spartothamnella*.

[4] Other transparent dots in the leaf are due to silicified groups of cells marking the position of hairs, which have fallen off (*Premna philippinensis*, Turcz.), or are caused by fissures produced in the leaf during drying (*Citharexylum cinereum*, L.) (Radlkofer).

of *Chloanthes*, such as *C. Stoechadis*, R. Br.; they envelop the greater part of the branch, and contain abundant assimilatory tissue with a system of vascular bundles, the whole being bounded on the outer side by an epidermis composed of large cells, which are mostly provided with a thick outer wall, while the epidermis on the inner side has thin walls, consists of small cells, and includes stomata. Distinct 'microptera,' which are T-shaped in transverse section, occur in *Xeroplana Zeyheri*, Briqu.; the same organs, but less strongly developed, are found in *Spartothamnella juncea*, Briqu., where they contain a bundle of sclerenchyma beneath the epidermis.

The development of the cork either takes place subepidermally (*Aegiphila*, *Citharexylum*, *Stachytarpheta* and *Vitex*, according to Vesque), or in the second or third cell-layer of the primary cortex (*Vitex* and *Citharexylum*, according to Möller), or deep in the primary cortex, a few cell-layers outside the pericycle (Stilbeae, according to Briquet). In the Chloantheae no cork is to be found in branches such as are preserved in herbarium-material (Briquet). The cork-cells have thin walls in *Citharexylum quadrangulare*, Jacq. and *Vitex agnus castus*, L.; in *Tectona grandis* some of them are strongly thickened on the internal tangential walls, whilst in *Petraea arborea*, H. B. K., they are tabular and thickened on the outer side (Möller). The presence of collenchyma in the primary **cortex** is not rare. An endodermis is wanting in most cases (Born). On the other hand, there are usually isolated bundles of hard bast in the pericycle; they sometimes almost become united to form a ring, and stone-cells may also appear in their neighbourhood, but a composite and continuous sclerenchymatous ring is rarely (*Petraea arborea*, *Avicennia*) present. Bands of bast-fibres with stone-cells are mentioned by Möller as occurring in the secondary bast of *Vitex agnus castus* and *Tectona grandis*, whilst Briquet states that 'scléréides' are present in the same region in species of *Eurylobium*, *Chloanthes*, *Pityrodia* and *Cyanostegia*; in *Chloanthes coccinea*, Bartl. and *Pityrodia Bartlingii*, Benth., almost the whole of the phloem, with the exception of the sieve-tubes, is sclerosed.

In the structure of the **wood**[1] the most important features are the simple pitting of the wood-prosenchyma and the constant presence (even in the herbaceous species, according to Born) of medullary rays. The latter are from one to six rows of cells in breadth. The size of the lumina of the vessels varies very considerably (maximum diameter = ·024–·18 mm.). The perforations of the vessels are generally simple. In *Stilbe pinastra*, L., *Campylostachys cernua*, Benth., *Chloanthes Stoechadis*, R. Br. and *Vitex saligna*, Roxb., the simple perforations are accompanied by others of the scalariform type which occur in the neighbourhood of the primary wood, or in the secondary wood itself also; some of these scalariform perforations exhibit an anomalous arrangement of the bars, and similar irregularities are recorded by Briquet in other Stilbeae and Chloantheae. Spiral thickening of the walls of the vessels and tracheids has been shown to occur in *Caryopteris Mastacanthus*, Schauer. In contact with parenchyma of the medullary rays the vessel-wall either bears bordered pits only, or (*Aegiphila*, *Congea*, *Symphorema*, *Vitex*) simple pits as well. Relatively strong development of the wood-parenchyma is only found in species of *Citharexylum*, where it occurs in the form of tangential bands (Möller), and in the spring-wood of *Tectona grandis*. The wood-prosenchyma bears simple pits, and is partly septate in species of *Aegiphila*, *Campylostachys*, *Chloanthes*, *Congea*, *Euthystachys*, *Lantana*, *Petraea*, *Stilbe*, *Symphorema* and *Vitex*. It remains to mention that in the heartwood of *Petraea volubilis*, *P. arborea* and *Tectona grandis*, considerable accumu-

[1] The statements in my 'Holzstruktur' are based on the examination of species of the genera *Stilbe*, *Campylostachys*, *Petraea*, *Vitex*, *Chloanthes*, *Lantana*, *Aegiphila*, *Caryopteris*, *Symphorema*, *Congea* and *Avicennia*.

lations of silica have been observed (Crüger). In *Petraea* they fill the lumina of all the elements of the wood, whilst in *Tectona* they only occur in the cavities of the vessels.

The **pith** is homogeneous in the Stilbeae (Briquet), heterogeneous in *Lantana Camara* (Mentovich); in *Phryma* the stem becomes fistular at an early stage; in the Chloantheae the pith rarely consists of cells with thin walls.

Anomalies in the structure of the axis are not common in this Order. Some of the lianes (*Petraea volubilis*, L. and species of *Lantana*, according to H. Schenck) have normal structure. Amongst the lianes an undetermined stem of *Lantana*, belonging to Schenck's collection (No. 654), has four deep furrows, corresponding to the orthostichies of the leaves. According to H. Schenck, the formation of furrows and the development of wings (which takes place in connexion with the former character) are still more typical in *Lantana lilacina*, Desf. The young axis of this species may have four of these wings or many, or the stem may be band-shaped. In stems which have attained a thickness of 3–4 cm., longitudinal fission into four segments, corresponding to the principal wings, takes place, probably as a result of torsion; these segments continue to grow in thickness by means of their cambium. Similar structural features are described by Fritz Müller and Crüger as occurring in certain undetermined climbing species of *Lantana*. An anomaly of another type is exhibited by the branches of the shrubby or arborescent species of *Avicennia* (*A. officinalis*, L. and *A. nitida*, Jacq., see De Bary, Wille and H. Schenck), viz. that of successive rings of growth [1]. The original ring of vascular bundles is limited externally by a composite and continuous sclerenchymatous ring, on the inner side of which the soft bast is situated; the latter, however, does not form a continuous annular zone, but occurs as isolated bundles, separated by lignified medullary rays, which constitute bridge-like connexions between the xylem and the sclerenchymatous ring. The first ring of bundles scarcely attains a thickness of ¼ mm. It is followed by parenchymatous tissue and then by the second ring of vascular bundles, which arises in an extrafascicular position and is adjoined externally by a sclerenchymatous ring, composed of from one to two layers of short cells. The first ring of growth is no broader than the original ring of vascular bundles, and its phloem is again differentiated in the form of cell-groups, separated by strips of woody tissue, which are composed of medullary rays, wood-prosenchyma and vessels, and connect the ring of xylem with that of the sclerenchyma. This is followed by a second and third secondary ring of growth, these being always narrow; all of them are extrafascicular in origin.

NOTE.—The negatively geotropic, **aerial roots** of *Avicennia officinalis* have been examined by Goebel and H. Schenck. Features which may be especially noted are the layer of cork, extending even over the apex of the root, and the formation of lenticels in this tissue; also the occurrence in the lacunar cortex of isolated cells having large lumina and walls provided with peculiar thickening ridges.

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[1] The anomaly occurring in *Avicennia* was quite incorrectly interpreted by Möller (Sitz.-Ber. Wiener Akad. 1876, pp. 31–5 and Tab.).

Bologna, 1886, p. 352 and tav. iii.—Radlkofer, Durchs. P., Sitz.-Ber. Münch. Akad. 1886, p. 326.—Petit, Pétiole, Mém. Soc. sc. phys. et nat. de Bordeaux, sér. 3, t. iii, 1887, pp. 353–4 and pl. vi.—Douliot, in Ann. sc. nat., sér. 7, t. x, 1889, p. 382[1].—H. Schenck, Luftw., Flora 1889, pp. 83–8 and Tab. iii.—Radlkofer, in Sitz.-Ber. Münch. Akad. 1890, p. 122.—Goebel, Pflanzenbiol. Schild. ii, Lief. 1, 1891, p. 13 and Tab. xii.—Schimper, Indo-malay. Strandfl., 1891, p. 17.—Solereder, *Melananthus*, Sitz.-Ber. deutsch. bot. Gesellsch. 1891, p. (72) note.—Zimmermann, Pflanzenzelle, 2. Heft, 1891, p. 137.—H. Schenck, Anat. d. Lianen, 1893, pp. 242–4 and Tab. xii.—Herbst, Markstr., Bot. Centralbl. 1894, i, pp. 403–4.—Briquet, in Natürl. Pflanzenfam., iv. Teil, Abt. 3 a, 1895, pp. 133–5.—Russell, Climat. méd., Ann. sc. nat., sér. 8, t. i, 1895, p. 343.—Briquet, Appareil végétatif des Phrymacées, Stilboidées, Chloanthoidées etc., Mém. Soc. phys. et hist. nat. de Genève, t. xxxii, 2e partie, 1896, sep. copy, pp. 5–79.—Warming, Halofyt Stud., K. Danske Vid. Selsk. Skr. 1897, p. 233.—[Solereder, *Buddleia Geisseana*, Bull. Herbier Boissier 1898, p. 624 et seq.]

LABIATAE.

1. Review of the Anatomical Features. A very characteristic feature of the Labiatae is the possession of ethereal oil, which is excreted mainly beneath the cuticle in various kinds of capitate hairs, and especially in the shortly stalked, bladder-like integumental glands (Fig. 152, *C–D*). In the capitate hairs the head is either unicellular, or divided by vertical walls only, as in the allied Orders. Other characters of importance in the anatomical diagnosis of the Order are as follows: the tendency to the formation of a characteristic type of stoma with subsidiary cells lying transversely to the pore (Fig. 152, *D*); excretion of oxalate of lime in the form of small needles, rods and plates, rarely as clustered crystals; perforations of the vessels mostly simple; wood-prosenchyma with simple pits and sometimes septate; and lastly the frequent development of typical collenchymatous tissue in the primary cortex, especially in the angles of the stem and branches. The place of origin of the cork is variable, and so is the structure of the pericycle (with regard to the presence or absence of an endodermis, or of primary hard bast). Apart from the external glands referred to above, the hairy covering consists of simple, unicellular and uniseriate trichomes, unicellular bracket-hairs, and branched hairs of varying structure. Special features are as follows: hypoderm in the leaf of *Rosmarinus*; resin-cells in the leaf of *Physostegia* and *Brazoria*; lamellated cork in *Sideritis*; and the occurrence of secondary groups of wood and phloem in the bast of old stems of *Thymus vulgaris*, L.

2. Structure of the Leaf. Considering the large size of the Order, which includes nearly 2,700 species, the leaf-structure has been little examined, and chiefly in a general comparative manner by Vesque. On the other hand, the hairy covering has repeatedly formed the subject of detailed investigations by Born, Hoch, C. Schmidt and others.

Regarding the ordinary leaf-structure, we need only mention that the mesophyll is either centric or bifacial, that the stomata are either restricted to the lower side of the leaf, or occur on both surfaces, and that the vascular bundles of the veins may or may not be accompanied by sclerenchyma. According to Vesque and others, *Rosmarinus officinalis*, L. possesses a hypoderm of large cells on the upper side of the leaf, vertically transcurrent veins, and branched spongy parenchyma. In most members of the Order the **stomata** are accompanied by two or more subsidiary cells, arranged transversely to the pore[2]. This type does not, however, as Vesque rightly pointed out, occur in all Labiatae. In *Teucrium Scordium*, for example, it is somewhat obscured by the presence of stomata bounded by several cells, accompanying those

[1] The '*Luhea speciosa*,' referred to by Douliot amongst the Verbenaceae, is a member of the Tiliaceae!

[2] In this case both the subsidiary cells and the mother-cell of the guard-cells arise from the initial cell by a series of divisions corresponding to the course of development, worked out by Strasburger in *Thymus serpyllum* and *Physostegia virginiana*.

with typical subsidiary cells, and this is still more pronounced in *Amethystea caerulea* and *Teucrium lucidum*. **Oxalate of lime**, when present in the leaf or axis, is excreted in the form of small acicular, rod-shaped, or octahedral crystals, which often occur in considerable numbers in the same cell; clustered crystals are rare (*Lycopus*, according to Briquet, *Pycnanthemum linifolium*, Pursh, according to Born). In the reproductive organs of the plant, clustered and ordinary solitary crystals appear to be more widely distributed than in the vegetative region; thus Briquet met with clustered crystals in the floral receptacle, and solitary crystals in the fruit of *Galeopsis*. The occurrence of large sac-like **secretory cells** in the mesophyll of the genera *Physostegia* and *Brazoria* is of special interest, because, as far as is known, the secretory system is entirely represented by external glands in the remaining members of the Order. The secretory cells of *Physostegia* and *Brazoria* give rise to transparent dots and striulations in the leaf. Höhnel first described them in *Physostegia virginiana*, Benth., where they form sacs about ·18 mm. long and ·008 mm. broad, and have suberized walls, two or three of them often being in lateral contact with one another. The secretory sacs which I found in *Physostegia intermedia*, Engelm. et Gray (Curtiss, n. 2051, Texas) and *Brazoria scutellarioides*, Engelm. et Gray (Lindheimer, Texas), have a similar structure.

The **hairy covering** is very varied and promises to afford valuable results for special diagnosis. Important features for the diagnosis of the entire Order are the frequent occurrence of clothing and capitate hairs side by side, and the fact that the capitate hairs, which for the most part have a glandular function, possess a uni- or multicellular head, divided, when multicellular, almost exclusively [1] by vertical walls. The ordinary form of clothing hairs consists of simple, uniseriate trichomes, unicellular hairs being rare in the Labiatae. The uniseriate hairs vary in length, sometimes only consisting of two, but often of many cells; the wall is either smooth, or provided with cuticular thickenings. The basal cell is commonly spherical and swollen, or (as in species of *Galeopsis* belonging to the section *Tetrahit*, species of *Stachys*, *Lamium*, *Origanum*, &c.) seated on a pedestal composed of several epidermal cells; sometimes (*Ballota*) the individual cells of the hair form distinct articulations. A special form of uniseriate hair is represented by bicellular trichomes with a short basal cell and a long terminal cell (species of *Betonica*, *Westringia*, &c.). According to C. Schmidt the bracket-hairs of *Mentha sativa* and *Ocimum basilicum* are special types of unicellular hairs. Branched or tufted multicellular trichomes have been met with in species of *Ballota*, *Betonica*, *Gomphostemma*, *Lavandula*, *Marrubium*, *Mentha*, *Nepeta*, *Phlomis*, *Rosmarinus*, *Stachys* and *Teucrium*; we shall now refer to those which have been more fully described.

The branched hairs of *Mentha rotundifolia*, Huds. have a uniseriate main axis, and lateral branches showing a similar structure but without special orientation (Briquet). In *Lavandula Stoechas*, L. only a few simple ray-cells are attached to the unicellular stalk (Briquet), whilst in *Lavandula vera*, DC. (Fig. 152 *A*) the branching is usually much more abundant. The hairs of *Teucrium Polium*, L. are similar to those of *Lavandula* (Born). In *Marrubium supinum*, L., *M. creticum*, 'And.', *M. candidissimum*, L., *Stachys affinis*, Fres. and *S. rugosa*, Ait. series of unicellular hairs, having their basal portions fused, are given off in 2–4 orthostichies from what may be described as the axis or prolongation of the stalk of the trichome; the terminal portion of the trichome is constituted by a long, multicellular hair; in *S. rugosa* the ramification may be repeated in the region of the terminal hair (Born). *Stachys aegyptiaca*, Pers. possesses trichomes, some of which are very similar to the hairs just described (Volkens, Fig. 152 *B*). The stellate trichomes of *Phlomis lanata*, Willd. consist of

[1] An exception is afforded by the stalked glandular hairs on the stamens of *Lamium album*, in which the head is divided by horizontal walls, or by both horizontal and vertical walls (Rauter).

a biseriate stalk, from the end of which 4–6 unicellular hairs radiate outwards. *Gomphostemma strobilinum*, Wall. has similar stellate hairs, but with a unicellular stalk.

The glandular hairs are just as varied in form as the clothing hairs, and several types may occur side by side in the same species. Every member of the Order probably possesses at least one type of glandular hair. Vesque's statement that external glands are wanting in '*Physostegia imbricata*,' which *is distinguished by the possession of secretory cells, is probably incorrect*; I have met with external glands both in the two species of *Physostegia* referred to above, and in a species of *Brazoria*, which is likewise distinguished by the possession of secretory cells. The glandular hairs may be classified in two groups, viz. (*a*) those which have a variously shaped glandular head, forming little or no

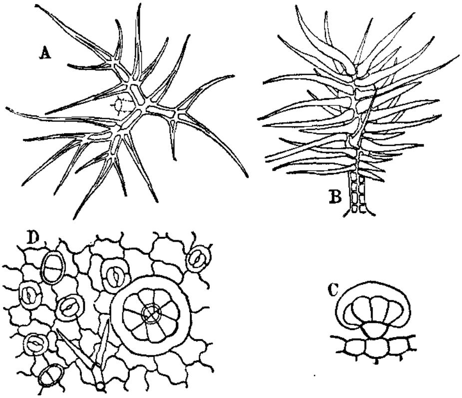

FIG. 152. Hairy covering of the Labiatae: A, C and D. *Lavandula vera*, DC. B, *Stachys aegyptiaca*, Pers.—A, C, D original, B after Volkens.

secretion below the cuticle, and (*b*) shortly stalked, bladder-like integumental glands, in which the cuticle of the glandular head is raised like a bladder, owing to the great accumulation of secretion. The latter type is specially characteristic of the Order. The external glands of the first category have a unicellular or uniseriate stalk of varying length and a spherical or ellipsoidal or disc-shaped head of varying size, the head being either unicellular, or bi- or multicellular, owing to the presence of one or a few vertical walls. The *bladder-like integumental glands are mostly inserted on the epidermis* by means of a short stalk-cell, and are commonly sunk in small pits on the surface of the leaf; they are usually divided by 4, 8, 16, &c., radial vertical walls, placed at right angles to the surface of the organ bearing the hair; more rarely the surface-view of the head shows a somewhat irregular arrangement of the cells, since all of them do not reach to the centre. I must not omit to mention that these bladder-like integumental glands, when depressed in small pits, sometimes give rise to transparent dots in the dried leaf, e.g. in *Monarda citriodora*,

Cerv., *M. punctata*, L., *Lycopus australis*, R. Br., *L. europaeus*, L., *L. lucidus*, Turcz., and in other cases (according to Radlkofer).

In order to make the reader acquainted with the forms of glandular hairs occurring in the Labiatae, Martinet's statements on this point may be mentioned[1]. The glandular hairs possess:

I. A unicellular head. External glands of this type, having a short stalk of from one to three cells, occur in the following species: *Lamium longiflorum*, *Lavandula vera*, *L. lanata*, *Melissa officinalis*, *Mentha citrata*, *Monarda didyma*, *Ocimum basilicum*, *Rosmarinus officinalis*, *Salvia glutinosa*, *Satureja montana*, *Scutellaria alpina* and *Thymus vulgaris*. A longer bicellular stalk, composed of a long basal cell and a short neck-cell, is found in *Horminum pyrenaicum*, *Lophanthus chinensis*, *Salvia Grahami*, *Sideritis hirsuta*, and others. Still longer stalks, though similarly uniseriate and provided with a short neck-cell at the apex, occur in *Ajuga pyramidalis*, *Lophanthus chinensis*, *Salvia chionantha* and *S. glutinosa*.

II. A bicellular head. Glandular hairs of this type are very common amongst the Labiatae; in some cases they have quite a short stalk of either one or two cells (species of *Dracocephalum*, *Elsholtzia*, *Hyssopus*, *Lavandula*, *Lophanthus*, *Nepeta*, *Perilla*, *Salvia*). A longer bicellular stalk, in which the upper cell is developed as a neck-cell, is found less commonly in these glandular hairs (*Stachys italica*, *Salvia glutinosa*); a still longer stalk is even rarer (*Ballota hirsuta* and *Scutellaria alpina*).

III. A head consisting of four cells. These glandular hairs are very widely distributed and invariably have short stalks. In some cases they produce abundant secretion, which accumulates beneath the cuticle. They may either be the only type of hair found in a species, or they may be accompanied by other glandular hairs with heads composed of more numerous cells; the first of these alternatives applies, for example, to *Salvia Grahami*, *Lamium album*, *Teucrium betonicum*, *Stachys byzantina*, *Leucas martinicensis*, *Ballota hirsuta*, *Galeopsis Ladanum*, *Marrubium leonuroides* and *Nepeta tuberosa*.

IV. A head composed of eight cells. Such glandular hairs are also frequent amongst the Labiatae, and mostly have very short stalks; some of them are differentiated as bladder-like integumental glands. They are not infrequently sunk in small pits on the surface of the organ. Glandular hairs of this type, but having longer stalks, composed of a long stalk-cell with or without short neck-cells, are rare (*Lavandula multifida*, *Salvia triloba*).

V. A head of sixteen or a still larger number of cells. Hitherto these glandular hairs have not often been met with amongst the Labiatae. Where they occur they either have a short or a very long stalk; both kinds occur in species of *Galeopsis* and *Scutellaria*.

It may be added that the leaf-teeth sometimes show glandular differentiation; e.g. according to Reinke in *Lamium album*, in which colourless mucilage-containing parenchyma occurs in the tips of the teeth together with the termination of a vein, and the epidermis lying above the latter contains a group of stomata.

The fibrovascular system of the **petiole** varies greatly. Commonly two vascular bundles enter the petiole, but they soon coalesce to form a single bundle; in other cases there is an arc of vascular bundles, their number being odd or even; more rarely the two vascular bundles or a single bundle may traverse the entire petiole. A ring of bundles does not occur in the petiole in any member of the Order. For details see Petit, and especially Briquet, who gives a detailed description of the structure of the petiole and the midrib of the leaf in the Labiates of the Maritime Alps[2].

3. STRUCTURE OF THE AXIS. The structure of the axis has been examined in special detail by Born; that of the Labiatae of the Maritime Alps has also been investigated by Briquet.

In all the members of the Order, and even in the herbaceous forms, the mass of **xylem** is traversed by medullary rays which are mostly narrow;

[1] Further statements on this subject contained in the literature are omitted, since, owing to the large size of the Order, their enumeration does not afford a complete record.

[2] Species of the genera *Mentha*, *Ajuga*, *Lycopus*, *Teucrium*, *Scutellaria*, *Galeopsis*, *Rosmarinus*, *Brunella*, *Stachys*, *Ballota*, *Dracocephalum*, *Lamium*, *Leonurus*, *Sideritis*, *Marrubium*, *Nepeta*, *Melissa*, *Hyssopus*, *Melittis*, *Satureja*, *Glechoma*, *Lavandula*, *Horminum*, *Origanum*, *Salvia* and *Thymus*.

more rarely (*Monarda mollis*, L., *Phlomis fruticosa*, L., *Plectranthus fruticosus*, L'Hérit., *Salvia officinalis*, L.) some of them are five or six cells in breadth; their cells are generally elongated in the vertical direction. The vessels are not large (maximum diameter = ·03–·05 mm.). The perforations are mostly simple; only in *Cymaria elongata*, Benth. have additional scalariform perforations been observed in the secondary wood; the bars in this case run at right angles to their usual direction. In contact with parenchyma of the medullary rays the walls of the vessels either bear bordered pits only, or (e.g. in species of *Salvia, Prostanthera, Westringia, Teucrium*) both bordered and simple pits. Spiral thickening occurs very commonly, but is almost always confined to the walls of the narrower pitted vessels and tracheids (e.g. in species of *Prasium, Prostanthera, Rosmarinus, Salvia, Sideritis, Teucrium, Thymus, Westringia*); more rarely it is also found in the vessels with wider lumina (*Prostanthera rotundifolia*, R. Br., *Westringia longifolia*, R. Br. and *W. rosmariniformis*, Sm.). The wood-parenchyma is not abundantly developed. The wood-prosenchyma appears to have simple pits. Septation of the lumen in the wood-fibres is mentioned by Born as occurring in species of *Plectranthus, Coleus, Hyptis, Lavandula, Gomphostemma, Phyllostegia, Prasium* and *Pogostemon*.

The **cortex** is especially distinguished by the frequent and often extensive development of collenchyma. Four subepidermal strands of this tissue situated in the four angles of the stems and branches are typical of the Order; they originate from special strands of meristem. The collenchyma is only rarely absent (in *Westringia rosmariniformis*, Sm., *W. longifolia*, R. Br. and *Prostanthera rotundifolia*, R. Br.). In the individual species the four bundles of collenchyma exhibit different aspects in transverse section. In some cases (*Horminum pyrenaicum*, L., *Leonurus Cardiaca*, L., *Lycopus*, &c.) additional smaller, subepidermal strands of collenchyma arise between the collenchymatous bundles in the corners and unlike the latter they are differentiated secondarily from the cortical parenchyma; in other cases a peripheral, closed, collenchymatous ring is found in the primary cortex (*Plectranthus, Coleus, Pogostemon, Collinsia, Phyllostegia*). With increase of age the cells of the collenchyma sometimes (*Salvia interrupta*, Schousb., *Monarda rugosa*, Ait., *Prasium majus*, L., &c.) become converted into sclerotic cells. In its remaining structural features the primary cortex shows variation. In the genus *Lavandula* it produces palisade-parenchyma; in *Marrubium vulgare*, L., the part of the cortex situated between the angles of the stem is differentiated into an outer layer containing chlorophyll, a middle collenchymatous layer and an inner band again containing chlorophyll; large intercellular spaces are found in the primary cortex in species of *Brunella* and *Stachys*, whilst an irregular hypodermal layer of large, lignified cells with thick walls occurs in *Prasium majus*, L., and so on. At the internal margin of the primary cortex an endodermis of thin-walled cells is commonly present; its cells either show Caspary's dots on the radial walls, or are completely suberized. Occasionally the endodermis is strengthened by the development of pericyclic hard bast, which in this case is generally present in small quantity; it rarely appears on the outer side of the endodermis (*Mentha sylvestris*, L., *Monarda rugosa*, Ait., &c.), more commonly on the inner side (*Mentha crispata*, Schrad., *Scutellaria peregrina*, L., &c.). In those members of the Order which have no endodermis, and this is especially the case amongst the woody species, the pericyclic hard bast is usually more strongly developed, but is very variable in its form and character. A transverse section of *Lavandula*, which belongs to this category, shows four well-developed semicircular groups of hard bast external to the four vascular bundles corresponding to the angles of the stem; between these groups there are smaller masses of a similar nature opposite the smaller vascular bundles. In the great majority

of the species without an endodermis the primary hard bast occurs in the form of irregular groups, which are often reniform in transverse section, the concavity sheltering a phloem-group of the vascular system. If one takes the whole Order into consideration, the soft bast of the four large vascular bundles, corresponding to the angles of the stem, is only in rare cases strengthened by connected masses of hard bast (species of *Hyssopus*, *Ocimum*, *Phyllostegia*, &c.), and still more rarely (species of *Ajuga*, *Cymaria*, *Marrubium*, &c.) do we find a continuous ring of primary hard bast [1]. In those cases in which the development of cork takes place on the inner side of the primary hard bast, the latter is thrown off with the primary cortex, and new groups of bast-fibres are then sometimes (*Rosmarinus officinalis*, L.) formed on the inner side of the cork by sclerosis of the adjacent cells of the soft bast; in *Salvia aegyptiaca*, L., the same process is repeated several times, so that a number of zones of cork and bast-fibres alternate with one another. According to Briquet sclerenchyma consisting of rod-cells occurs in the secondary bast in *Ballota frutescens*, Woods.

The development of the **cork** varies. It is formed subepidermally in *Coleus Wightii*, Benth., *Plectranthus fruticosus*, L'Hér., *Stachys rugosa*, Ait., *Leonurus Cardiaca*, L., according to Born, and in *Salvia aurea*, *Pogostemon plectranthoides*, and *Sideritis canariensis*, according to Petersen. The cork of *Sideritis canariensis* is lamellated; first a few layers of cork-cells are developed from the subepidermal layer; then the cork-cambium ceases to be active, and the second cell-layer of the primary cortex gives rise to a second cambium, which forms another cork-lamella, and so on. According to Petersen the cork is developed in the middle of the primary cortex in *Phlomis tuberosa*, whilst in *Hyssopus officinalis*, L. its position is immediately external to the endodermis, according to Briquet. Petersen has described pericyclic development of cork internal either to the endodermis, or to the primary groups of hard bast, in species of *Ballota*, *Lavandula*, *Micromeria*, *Origanum*, *Rosmarinus* and *Sphacele*; the same feature was observed by Born in species of *Leonotis*, *Plectranthus*, *Prasium*, *Salvia*, *Stachys* and *Teucrium*, and by Briquet in species of *Satureja* and *Sideritis*. According to Born, *Thymus vulgaris*, L., *T. villosus*, L., *T. pannonicus*, All., *Origanum Majorana*, L., *O. Onites*, L., and *Satureja Thymbra*, L., exhibit a special mode of cork-formation without the development of a phellogen; in these species the cells situated on the inner side of the suberized endodermis gradually undergo complete suberization, the process commencing in the cells next the endodermis and advancing towards the cambium.

The course of the **vascular bundles** in the stem of the Labiatae may be described as follows (for details see Nägeli, Guillard and Briquet). From each leaf two vascular bundles usually enter the stem, where, diverging from one another, they pass down through the next internode in the two angles of the stem situated on the right and left of the leaf. In the next internode they run beside the leaf-trace bundles entering the stem at the second node, and fuse with them at the following (third) node. It may also be mentioned here, that according to Bonnier old stems of *Thymus vulgaris*, L., from the Pyrenees (but not from other localities), exhibit strikingly eccentric growth in thickness and subsequent formation of new strands of wood and phloem in the secondary bast.

The **pith** is described by Briquet as being homogeneous in many members of the Order; in the herbaceous species it commonly breaks down.

Literature: Nägeli, Beitr. z. wiss. Bot., 1. Heft, 1858.—Kirchhoff, De Labiat. org. veg., Diss.,

[1] Regarding the distribution of endodermis and pericyclic hard bast, which is generally speaking only of importance for specific diagnosis, see Born's synopsis, loc. cit., pp. 32–5, and Briquet, Labiées des Alp. mar.

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PLANTAGINEAE.

Of the three genera composing this Order, *Plantago* and *Litorella* have been investigated. They are specially distinguished by two features, viz. (*a*) glandular hairs, the heads of which, as in the Labiatae and Verbenaceae, are mostly divided by vertical walls only; (*b*) a stomatal apparatus exhibiting a tendency towards the Caryophylleous type. Other features of importance for the diagnosis of the Order are as follows: oxalate of lime has not been observed; medullary rays are not present in the wood (even in the shrubby species of *Plantago*); in the woody species of *Plantago* the mass of xylem is composed of vessels with small lumina and simple perforations, of tracheids, and of wood-prosenchyma with simple pits, forming the greater part of the wood; finally, the formation of cork is superficial. The occurrence of small medullary and cortical cambiform strands or vascular bundles in the stem of certain species of *Plantago* is specially noteworthy.

The anatomy of the **leaf** in the genus *Plantago* may be described as follows, on the authority of Vesque. The leaf-structure varies, being often centric, especially in species with acicular leaves (e.g. *P. aristata*, *P. Cynops* and *P. subulata*), but also in *P. maxima*, whilst it is bifacial in *P. lanceolata* and *P. media*. The **stomata** occur on both sides of the leaf. The prevalent type of stoma is that found in the Caryophylleae, the pair of guard-cells being accompanied by subsidiary cells placed transversely to the pore (*P. aristata*, *P. Cynops*, *P. lanceolata*, and *P. subulata*). In many cases, however, and sometimes even on the same leaf, the Caryophylleous type is more or less obscured, but *P. media* was the only species where Vesque did not meet with a single stoma in which the type in question was well marked. The **hairy covering** in the species of *Plantago* consists of simple, uniseriate trichomes (Fig. 153, *A–B*) and glandular hairs. The former have been examined in detail by Cugini and Volkens. They exhibit a series of variations in the number, length, and mode of connexion of the cells forming the hair, and in the nature of the surface, thickness of the wall and width of the cell-lumen. The trichomes may be either composed of a considerable number of cells or of only a few. Hairs with few cells, consisting

only of one or two short basal cells, and a long sword-shaped terminal cell, are found, for example, in *Plantago arctica*. The cells of the hair may have either thick or thin walls; their surface may be smooth, striated, or covered with punctiform or verrucose prominences. The terminal cells are not uncommonly shorter, and have considerably thicker walls than the remaining cells of the hair. The mode of attachment of the cells of the hair to one another is interesting in certain species. In most cases the cells are separated from one another by cross-walls, placed at right angles or nearly so to the longitudinal axis of the trichome. In *P. argentea* (Fig. 153, *A*), *P. lanceolata* and *P. montana*, however, there are sympodial trichomes in which the division-walls between the cells of the hair are strongly inclined, the inclination being always in the same direction; the apices and bases of successive cells overlap one another for a short distance, and this too always takes place in the same direction. Even more remarkable are the trichomes observed by Cugini in *P. lanceolata*; in these hairs, which occur intermingled with other forms, the contiguous ends of the cells are forked and dovetailed with one another. In the trichomes which Volkens found in *P. cylindrica*, Forsk. (Fig. 153, *B*) and *P. ovata*, Forsk., the number of dovetailed prolongations of the cells is still greater. The object of this arrangement no doubt consists in the establishment of a firm connexion between the frequently elongated cells, to form the long trichome. In the case of the glandular hairs which Vesque observed in *P. Cynops*, *P. arenaria*, and *P. media*, he describes a uniseriate stalk and a bicellular head, divided by a vertical wall. Cugini figures external glands in *P. lanceolata* with a sac-like, ellipsoidal head possessing vertical and horizontal division-walls. The structure of the **petiole** varies greatly in the species of *Plantago*, and it will be possible to make use of it for special diagnosis. The vascular bundles of the petiole are isolated in all the species examined, and alternate with much smaller bundles, both series together forming an arc. The number of larger bundles varies: 5 in *P. lanceolata*, 7 in *P. media*, 11–13 in *P. maxima*. In the species with large leaves each vascular bundle has the shape of an arc, and is supported above and below by mechanical tissue.

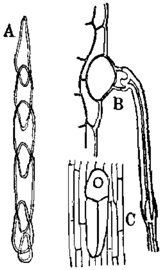

FIG. 153. Trichomes of the Plantagineae. A, *Plantago argentea*; B, *Plantago cylindrica*, Forsk.; C, *Littorella lacustris*, L.—A after Cugini, B–C Original.

The following account of the foliage leaf of *Littorella lacustris*, L. is based on the statements of Areschoug, Kutsomitopulos and H. Schenck. Three vascular bundles traverse the mesophyll, which beneath the epidermis consists of one or two fairly dense layers of cells, containing abundant chlorophyll, whilst the inner portion of the mesophyll is composed of a network of cells with less chlorophyll. The polygonal air-cavities, several series of which are irregularly arranged about the centre of the transverse section of the leaf, are separated by single layers of parenchymatous cells. The epidermis of the leaf consists of narrow, four-sided cells, elongated in the direction of the veins. In the land-forms it bears numerous stomata, arranged in longitudinal rows, on both sides of the leaf; in the water-forms stomata are rare. The stomata of *Littorella* show at least some indications of the Caryophylleous type, for an epidermal cell adjoins each of the narrow ends of the pair of guard-cells. The occurrence of glandular hairs (Fig. 153, *C*) on the leaf is very characteristic. They possess a very short basal cell, on which the trowel-shaped head is inserted excentrically and horizontally; the head is divided by a vertical wall parallel to its shorter diameter into

a posterior smaller cell, seated on the stalk, and an anterior larger segment, which becomes further subdivided into two cells by a vertical wall parallel to the longer diameter of the head.

The structure of the **stem** in the genus *Plantago* has been subjected to a detailed examination, especially by Kuhlmann. The constant feature in the structure of the wood consists in the absence of medullary ray tissue. In the woody *Plantago Cynops* the xylem is composed of vessels with small lumina and simple perforations, tracheids, and principally wood-fibres bearing simple pits[1]. In the herbaceous species the ground-mass of the wood as a rule consists of unlignified parenchyma. In certain species (e.g. *Plantago media*) the outer portion of the ring of bast is thickened, but not lignified, and serves as mechanical tissue. In *Plantago Cynops* it consists of lignified, elongated, parenchymatous cells. In the annual species, such as *P. arenaria* and *P. Psyllium*, the vascular ring is surrounded by a sclerenchymatous zone, composed of two or three layers of lignified and strongly thickened bast-fibres. The formation of cork usually commences in the outermost cell-layer of the primary cortex, but in *P. Cynops* at a depth of four or five layers beneath the epidermis. The following special anatomical features are found in the stem of species of *Plantago*: medullary and cortical bundles of cambiform tissue, the development of bark, and the occurrence of stone-cells in the ground-tissue. Both medullary and cortical cambiform strands (Sanio, Kuhlmann) occur in *P. major* and *P. media*, cortical strands only in *P. lanceolata*. The cambiform strands[2] consist of long and narrow cells with abundant protoplasm; they appear to contain no sieve-tubes. The bundles are of secondary origin, and are connected with one another, but not with the bundles of the vascular ring. In specially strong root-stocks of *P. major* and *P. media* the cambiform strands become transformed into vascular bundles, consequently they may also be described as reduced vascular strands. Here we may mention the statements of Reiche and Harms that cortical vascular bundles and medullary phloem-bundles occur in *P. fernandezia*, Bert. The development of bark has been recorded by Kuhlmann in *P. maritima*, *P. alpina*, *P. atrata* and *P. Coronopus*; it may be either ring- or scale-bark. The same author mentions the occurrence of nests of stone-cells in the pith and outer cortex of *P. lanceolata*, and in the pith of *P. montana* and *P. saxatilis*, and that of a few stone-cells in the pith of *P. victorialis* (cf. also Dutailly, loc. cit.).

A transverse section through the small stem of *Littorella lacustris* shows a ring of vascular bundles, large schizogenous intercellular spaces in the primary cortex and subepidermal development of cork.

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[1] The statement of Kutsomitopulos, that the wood of *P. Cynops* consists of vessels and tracheids only, is incorrect.

[2] Dutailly incorrectly describes them as 'réseau de canaux sécréteurs à segmentation périphérique.'